

BULLETIN
of **CARNEGIE MUSEUM OF NATURAL HISTORY**

**THE COMPARATIVE SOCIAL BEHAVIOR OF
KERODON RUPESTRIS AND *GALEA SPIXII* AND THE
EVOLUTION OF BEHAVIOR IN THE CAVIIDAE**

THOMAS E. LACHER, JR.

*Department of Biological Sciences, University of Pittsburgh,
Pittsburgh, Pennsylvania 15260 and
Pymatuning Laboratory of Ecology,
Linesville, Pennsylvania 16424*

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ABSTRACT

I conducted an 18 month study on the behavior and ecology of two species of sympatric caviid rodents (*Kerodon rupestris* and *Galea spixii*) in northeastern Brazil. Preliminary observations indicated that *Kerodon* was a habitat specialist, occurring only in large boulder piles, whereas *Galea* appeared to be a habitat generalist, occurring in a variety of open habitats excepting the boulder piles inhabited by *Kerodon*. This situation presented an ideal field experiment to compare the social structures in these two closely related genera.

I first established breeding colonies of both in order to describe their behavioral displays and to discern their function. Complete behavioral repertoires, including vocalizations, are presented for both *Kerodon* and *Galea*.

Reproduction and growth, behavioral development, sexual behavior, agonistic behavior, and use of space were all examined both quantitatively and qualitatively in the colonies and in the

field. Time budgets were calculated and analyzed for both genera. Differences in rates of growth and behavioral development between the two genera are probably related to ecological aspects of their significantly different microhabitat preferences. Data on sexual and agonistic behavior collected in the colonies suggested that *Kerodon* exhibited resource defense polygyny, whereas the *Galea* mating system approximated male dominance polygyny. Field data supported the colony observations. These differences in mating systems may be related to the different habitat preferences observed. *Kerodon* is compared to other resource defense polygynists.

Finally, a model for the evolution of behavior in the family Caviidae is presented. The social organizations of the various genera seem to be very responsive to ecological requirements. The importance of social organization in ecological adaptation is discussed.

INTRODUCTION

Morphology, physiology, and behavior all play a role in the adaptation of an organism to its environment. Morphological and physiological adaptations, as well as behavioral displays, seem to have evolved in response to average long term environmental influences. Skeletal morphology, for example, seldom shows seasonal variations; basic behavioral gestures are generally quite consistent within a species from one geographical locality to another (Eisenberg, 1967). Social behavior, however, is far more labile in its response to the environment (Stacey and Bock, 1978), and in conjunction with mating strategies, may well represent the means by which organisms keep their reproductive success high in the face of short term environmental fluctuations. One of the most effective techniques for assessing the adaptive value of social organization is the analysis of behavior of closely related species occupying markedly different habitats.

Eisenberg's (1963, 1967) work on the behavior of heteromyid, murid, and dipodid rodents is an excellent example of the use of a comparative study to explain behavioral repertoires from an adaptive, evolutionary perspective. Two major concepts that emerged from this work which should be considered in any comparative behavioral study are: 1) "discrete behavior patterns exhibit a profound similarity"; and 2) "differences in the frequency of occurrence rather than in the form of the movement have proved to be the most effective criterion for delineating taxon-specific differences." Subsequent comparative studies on mammals have reinforced

these concepts both for behavioral repertoires (Rood, 1972; Kleiman, 1974; Wilson and Kleiman, 1974) and for vocal repertoires (Eisenberg, 1974).

Behavioral research on mammals has most recently been concentrated in two groups—the higher primates in general, and the South American caviomorph rodents. The interest in the caviomorph rodents is due in part to their substantial morphological variability (Walker, 1974) and the wide variety of habitats that they occupy (Osgood, 1943; Moojen, 1952; Cabrera and Yepes, 1960). The caviomorphs diversified greatly from the Oligocene through the Pleistocene when other rodent competitors were absent (Simpson, 1945; Landry, 1957; Mares, 1975). Eleven families and forty-six genera are currently found in South America (Simpson, 1945), and their habitats range from fossorial (*Ctenomys* and *Clyomys*) to semi-aquatic (*Hydrochoerus* and *Myocastor*) to arboreal (*Coendou*, *Kerodon* and various echimyids). Caviomorphs are found in all major South American habitat types including Tropical Forest, Savannah, Cerrado, Caatinga, Temperate Forest, Chaco, Llanos, Desert and Puna biomes. This morphological variability, coupled with the diversity of habitats, has led to the evolution of many interesting ecological and behavioral adaptations (Eisenberg, 1974; Kleiman, 1974). The caviomorphs, for these reasons, offer excellent opportunities for behavioral studies of a comparative nature.

The family Caviidae contains six genera and approximately twelve species and has undergone an

interesting radiation. There are two distinct subfamilies—the Dolichotinae, which includes the genera *Dolichotis* and *Pediolagus*; and the Caviinae, which contains four genera, *Kerodon*, *Galea*, *Cavia*, and *Microcavia*.

The dolichotines are hare-like in their external morphology, and inhabit open semiarid grasslands, xeric thornscrub, and temperate steppe in Argentina and southwestern Paraguay. The basic social unit of the dolichotines is the pair, and after parturition a temporary family unit is formed that persists from 6 to 8 months. In addition to possessing most of the typical caviomorph behavioral repertoires, the dolichotines also show many behavioral adaptations similar to those of the large African herbivores (Cabrera, 1953; Dubost and Genest, 1974; Kleiman, 1974).

In contrast to the dolichotines, the subfamily Caviinae contains the more familiar "Guinea-pig" like rodents. *Microcavia*, *Cavia*, and *Galea* are all quite similar in morphology, resembling the common laboratory *Cavia porcellus* in body form. The genera differ primarily in size and in characteristics of the pelage. All three genera have four clawed digits on the manus and three clawed digits on the pes, and have a plantigrade foot posture. *Galea* is easily distinguishable from the other two genera by the presence of yellow incisors. These three genera occupy, in general, more open formations, ranging from *Larrea* flats (*Microcavia*) to open pampas (*Cavia*), or thornscrub forest and high Andean grasslands (*Galea*). All possible pairs of these three genera occur sympatrically in certain parts of their distributions. In certain areas of northeastern Argentina, all three genera may be sympatric (Cabrera, 1953; Contreras, 1965; Rood, 1972; Vaughan, 1972).

Kerodon has the same basic caviine body form as the above three genera, but possesses some morphological and cranial characteristics unique to the subfamily. The manus and pes are padded with a leather-like epidermis (very similar to the feet of hyraxes) and claws are absent. The feet have subcutaneous nails on all digits but the innermost digit of the pes, where the nail has been modified as a small grooming claw used to comb the pelage.

Kerodon is restricted in distribution to terrestrial islands of granitic boulders which occur throughout the Caatinga, a semi-arid region in Brazil. Animals use fissures and hollows in the rocks for shelter and to escape from predators, and emerge throughout the day and night to forage in the adjacent trees and shrubs. They are extremely agile climbers, which

is unusual considering that they have neither claws nor a tail, two adaptations normally associated with arboreality. The skull, especially the rostrum, is longer and narrower than in other caviines, and the distance between the incisors and the premolars is proportionately greater (Moojen, 1952; Walker, 1974).

The phylogenetic relationships of the caviids are still unclear (Patterson and Pascual, 1972; Spatorno, 1979). The family is first known from the mid-Miocene, and by late Miocene the two subfamilies had separated (Landry, 1957). The current genera had probably all evolved by the mid-Pleistocene (Rood, 1972). Pascual (1962) divides the subfamily Caviinae into four groups based on molar characteristics—an extinct *Allocavia* group; a *Cavia* group, which includes *Cavia* and the extinct genus *Paleocavia*; a *Microavia* group; and a *Galea* group, which also includes the genus *Kerodon*. Of the current genera of Caviinae, only *Galea* and *Kerodon* are classified in the same group. *Kerodon* is seemingly more closely related to *Galea* than to any other caviid.

The caviids have been fairly well studied behaviorally. Both the dolichotines (Smythe, 1970; Dubost and Genest, 1974; Wilson and Kleiman, 1974) and the caviines (King, 1956; Kunkel and Kunkel, 1964; Rood, 1970, 1972) have been observed under at least seminatural conditions, and complete behavioral repertoires are present for all caviid genera except *Kerodon*. An examination of the behavior and ecology of *Kerodon* is therefore essential in any attempt at understanding the evolution of social behavior in the Caviidae.

In this study the behavior of *Kerodon* is compared with the behavior of *Galea spixii spixii* (Wagler), a species sympatric with *Kerodon* in certain areas of northeastern Brazil. *Kerodon* is restricted to the semiarid Northeast, however, whereas *Galea* has a far more extensive distribution, occurring in Caatinga, the semiarid habitat of the Northeast; in the more mesic Cerrado savannahs; in Agreste, transition between Caatinga and Atlantic forest; and in the more open sections of Atlantic rain forest. In comparison with *Galea*, therefore, *Kerodon* is a habitat specialist, restricted entirely to a potentially physiologically taxing environment. *Galea* is clearly a habitat generalist, occurring in a variety of open formations. This study focuses on the behavioral repertoires, foraging behavior, patterns of aggression, mating systems, and social organization of both species. I then attempt to relate differences

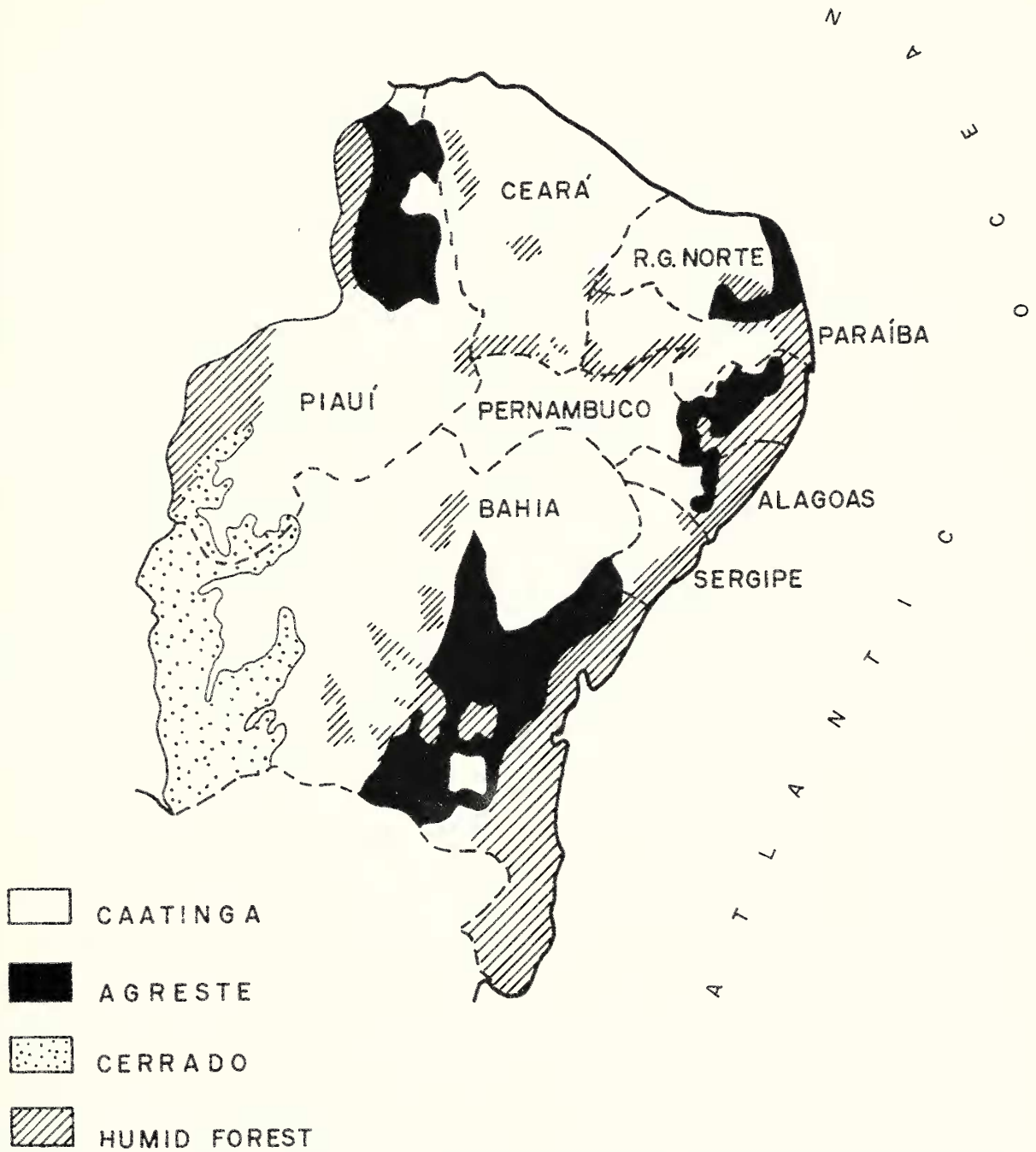


Fig. 1.—Major vegetational formations in the eight states that comprise northeastern Brazil. Modified from Carvalho (1973).

in social behavior to differences in ecology, specifically in relation to the different habitat requirements of the two species.

Many important parameters that we use to define an organism's niche are primarily behaviorally determined (for example, feeding preferences and for-

aging behavior, choice of burrows or nesting sites, territoriality, reproduction and courtship, activity patterns, and microhabitat selection). Simpson (1958) stated that behavior is "the actual means of interaction between physical organization and the environment, hence the direct and visible expres-

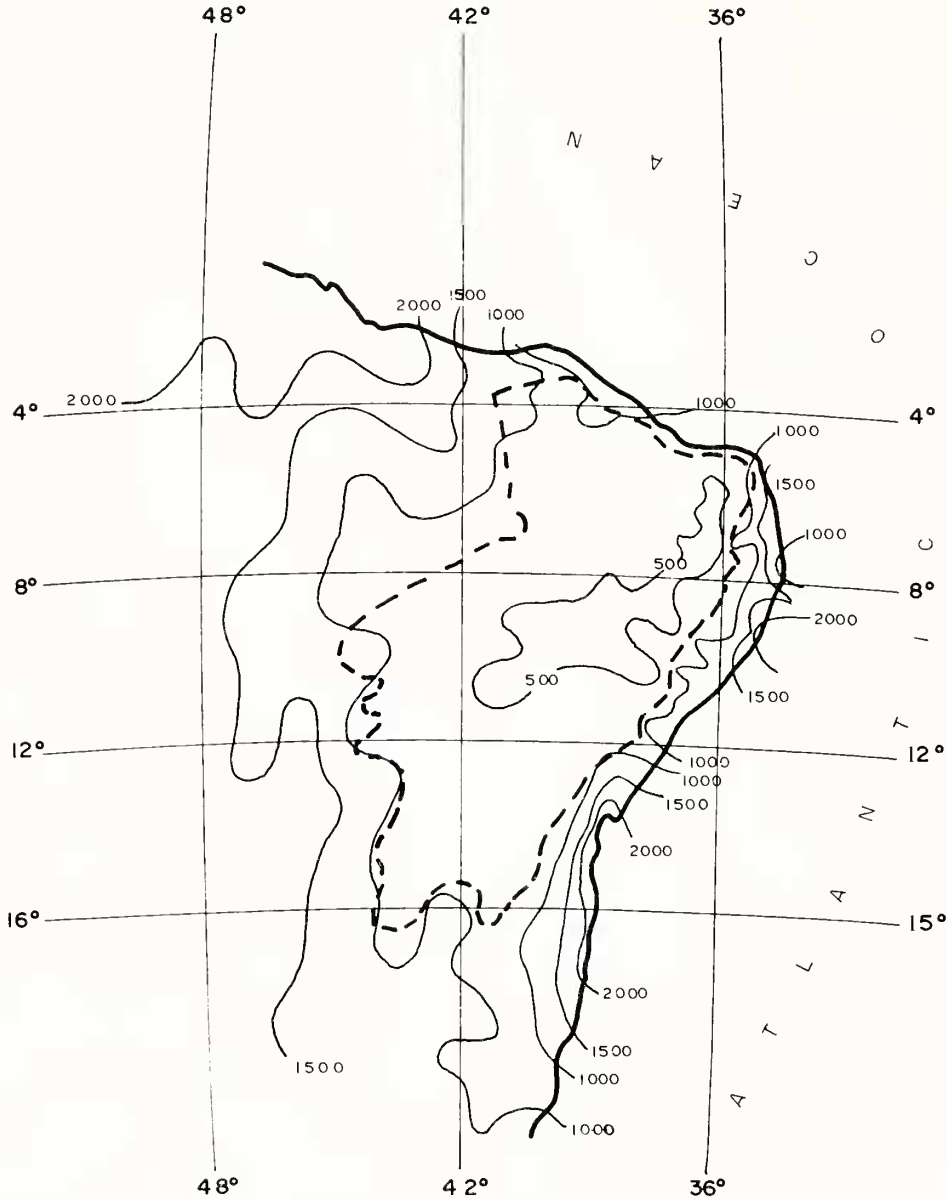


Fig. 2.—Annual rainfall in northeastern Brazil. Values are reported in mm. The limits of the Caatinga (dotted line) approximately follow the 1,000 mm isohyet. Modified from Souza Reis (1976).

sion of the relationship that is adaptation." This study offers the opportunity to evaluate the adaptive importance of social behavior in two closely-related organisms with differing ecological requirements.

Data collected on the ecology and social behavior of *Kerodon* are, in addition, compared to certain aspects of the behavior of the other caviids. Finally I attempt to clarify the trend of evolution of social behavior for this family.

GENERAL HABITAT DESCRIPTION

The Caatinga (Fig. 1) covers an area of 650,000 km² between 3° and 16° South Latitude and 45° and

35° West Longitude in the northeastern corner of Brazil (Frota-Pessoa et al., 1971; Souza Reis, 1976).

The annual rainfall of the Caatinga varies from slightly over 1,000 mm to less than 400 mm (Fig. 2). The region is not dry enough to be classified as a desert, but because of anomalies in yearly precipitation, it is susceptible to serious droughts and flooding (Eidt, 1968)

Physically, the Caatinga is dominated by three major elements—1) a basement of pre-Cambrian crystalline rocks which, when exposed, form a surface of gentle slopes; 2) many groups of hills, and ranges of low mountains of granitic rock (*serras*) which are the products of erosion and denudation; and 3) a cover of sandstone strata which at one time covered most of the crystalline basement, but is now partly stripped off by post-Cretaceous erosion. This sandstone layer, when eroded, forms the mesa-like plateaus known as chapadas (James, 1942; Ab'Saber, 1970). More information on the climate and geology of the Caatinga can be found in Vasconcelos Sobrinho (1971), Markham (1972), and Carvalho (1973).

The zoogeographic relationships of the Caatinga are poorly understood. Sick (1965) and Vanzolini (1974, 1976) have indicated that the Caatinga, as well as the intervening Cerrado, have very low rates of endemism. Both areas appear to have been colonized by tropical elements from the Amazon Basin (north and west) and the Atlantic rainforest (east), and by scrub and semitropical elements from the belt of Caatinga, Cerrado, and Chaco, which runs southwesterly to Paraguay and Argentina. Guima-

rães (1972) reports that the mammalian faunas of the Caatinga and Cerrado have many species in common. Vanzolini (1976) has compared the lizard faunas of the Cerrado and Caatinga, and reported that species compositions were virtually identical. The one endemic Caatinga lizard, *Platynotus semi-taeniatus*, is associated with peculiar granitic rock formations that occur extensively throughout the Caatinga, and are known as lajeiros (extensive exposed tables of the crystalline basement, which often have large piles of boulders scattered upon their surface). Data on mammal distribution patterns suggest that *Kerodon rupestris*, which occurs in the same habitat, is also a Caatinga endemic (Cabrera, 1953; Walker, 1974).

My field site, Fazenda Batente, is a privately owned farm located in the municipality of Exu, 6 km SE of the town of Exu, Pernambuco, Brazil. Although Exu is located near the center of the Caatinga, it receives more rainfall than areas 20 to 30 km to the south, being situated at the southern base of the extensive plateau system of the Chapada do Araripe, which is one of the major centers of orographic rainfall in the Caatinga (Markham, 1972). The amount of rainfall received in the low areas decreases as one moves south from Exu. The vegetation of the Exu region, therefore, contains some Cerrado elements not normally found in Caatinga associations, while it lacks various species common in the more arid regions to the south.

MATERIALS AND METHODS

HABITAT ANALYSIS

The study site contains a series of large boulder piles and lajeiros (rock faces) separated by patches of scrub forest, cacti, and second growth vegetation (Figs. 3 and 4). During the peak of the rainy season, samples of leaves, buds, and flowers of all species of plants present on the area were collected. These included not only trees and shrubs, but also cacti and all grasses. These were taken to the Instituto de Pesquisas Agronômicas in Recife, Pernambuco, for positive identification. The various microhabitats present on the study areas were then visually separated as to their most common plant form and species. These classifications were subsequently used to examine microhabitat associations of the mammal fauna via mark and recapture data.

A maximum-minimum thermometer was set up in the middle of the study area and a year-long record of weekly temperature minima and maxima was made. In addition, the relative humidity was recorded with a sling psychrometer on the morning of every trapping day. General weather conditions were also noted daily.

COMPARATIVE BEHAVIOR AND ECOLOGY

Colony Studies

Breeding colonies were set up for both *Kerodon rupestris* and *Galea spixii spixii*. Animals for both colonies were captured in the wild at a variety of localities in northwestern Pernambuco.

The *Kerodon* colony was established 4 February 1977 with the introduction of two adult males, three adult females, and one subadult female. The first litter was born in late July 1977. The colony increased in size to a maximum of 17 in March 1978, and contained 14 animals on the date of termination, 26 March 1978. The colony was maintained in a large (25 m by 10 m) windowed laboratory room of an abandoned agricultural school in Exu. Prior to the introduction of the animals, the room was divided into four subareas, each of which was modified to mimic a microhabitat available to *Kerodon* on the study site. Two areas (15 m by 5 m each) were altered to resemble a boulder strewn rock-face and a dry, shallow-soil scrub forest. The other two



Fig. 3.—Map of the Fazenda Batente study area, indicating major rock piles. Study area subdivisions are indicated by roman numerals. Arabic numbers indicate trap sites and microhabitat type. The area was bordered on the east by cornfields, the west by a fenced corral, the north by a small stream and the south by a dirt road. Microhabitat code: 1 = *Croton* thickets; 2 = level shrub and grass areas; 3 = boulder, cacti areas; 4 = cultivated area; 5 = *Cnidocolus* flat; 6 = *Jacobinia*, *Ruellia* flat. Distance from fence to beginning of cornfields is about 80 m.

areas (10 m by 5 m each) were modified to resemble a grassy field and a brush tangle, two microhabitats that are fringe habitats for *Kerodon*, but preferred habitats for *Galea*. These areas were included in the *Kerodon* colony room to observe the degree of utilization of these habitats by *Kerodon* during normal daily activity.

Throughout the course of the study, *Kerodon* were presented a diet of green vegetation and pineapple, occasionally supplemented with dried corn and Brazil nuts; water was provided ad libitum. All of the plants selected were common in *Kerodon* habitat, and included *Cassia excelsa* (Leguminosae), *Ziziphus joazeiro* (Rhamnaceae), *Solanum paniculatus* (Solanaceae), *Croton campestris* (Euphorbiaceae), and *Brachiaria nutica* (Graminae).

The *Galea* colony was established on 3 September 1978 with the introduction of four adult females, two subadult females, three adult males, and two subadult males. The two subadult males were the progeny of one of the adult females. The first birth in the colony occurred in late November, and reproduction continued until the end of the study on 26 March 1978. Colony size peaked twice at 15, in early February and in late March. The *Galea* were also maintained in a windowed laboratory room (10 m by 8 m) of the agricultural school. The room was altered primarily to mimic *Galea* habitat; however, rocks and trees were added to determine if they were utilized in the absence of *Kerodon*. The animals were provided with water, pineapple, and green vegetation, primarily *Brachiaria*, and, occasionally, *Croton* or *Cassia* (*Brachiaria* was highly preferred).



Fig. 4.—View of the major rock pile of subdivision II and associated vegetation. *Kerodon* dwell in the cracks between the boulders.

General observations were taken in the same manner on both colonies. The animals were all individually marked with a commercial fur dye, Jamar D. Observations were made from outside the colony through an open shutter. Because both species are active throughout the day, with a slight depression in the level of activity during the mid-day hours, observations were concentrated during the morning and evening hours, and, in the case of *Galea*, at night. All behaviors observed were recorded, many postures being sketched upon observation. Additional sketches were made from numerous still and motion picture films. Both 8-mm and 16-mm movies were taken during general colony activity and in encounter situations. These general observations were used to establish the basic behavior postures and displays, and to clarify the overall patterns of social behavior of each species.

Throughout the period that the colonies were maintained, reproductive and growth data were collected on all animals. Animals were captured, weighed, checked for reproductive condition, and redyed once each month. When females neared the end of their gestation, they were captured and palpated daily. On the day of birth, the female was captured, weighed, and checked for signs of copulation. Numerous copulations occurred on the day of birth, and in situations where copulations were not directly observed, the females were found to have either copulatory plugs or semen present in the vagina. As both species exhibit a postpartum estrous, gestation periods were calculated from the day of birth. The newborn juveniles were also captured,

sexed, measured, and weighed at five-day intervals until 30 days of age, and then at 10-day intervals until 120 days of age. Beyond this, animals were handled only during the monthly weighings. The growth data on juveniles were then plotted and a regression line fitted to the data in order to calculate a growth equation (Lacher, 1979).

An additional aspect of the comparative behavioral study was an examination of the interspecific interactions, which occurred in a mixed colony of the two genera. Three separate mixed colonies were observed for a period of 4 to 6 days each—one in which both *Kerodon* and *Galea* were introduced simultaneously; a second where *Galea* were introduced into the existing *Kerodon* colony; and a third where *Kerodon* were released into an existing *Galea* colony. Animals were again dyed for individual identification. Density of animals per m² of colony floor was kept constant for all three situations so as not to alter aggressive levels artificially. Observations of one hour's duration were conducted from one to three times daily, during which all interspecific and intraspecific aggressive and sexual interactions were recorded. The number of aggressive encounters was then standardized to a per hour rate, so that the day to day trends in inter- and intraspecific interactions could be interpreted.

Patterns of aggression were also examined in the individual colonies. For all aggressive encounters observed, the aggressive and submissive individuals were identified, and the type of aggressive display, as well as the corresponding subordinate response, were noted. These data were then used to compare the

overall patterns of aggression within each species in relation to its social organization. The data used in this comparison were collected simultaneously for both colonies between September 1977 and April 1978.

Time budget data were collected on six separate groups—adult male *Kerodon*; adult female *Kerodon*; juvenile male *Kerodon*; juvenile female *Kerodon*; adult male *Galea*; and adult female *Galea*. Time budgets were obtained in the same manner for both *Kerodon* and *Galea* excepting the time of observation. *Kerodon* time budgets were obtained in the morning, between 7 and 10 AM, whereas *Galea* time budgets were calculated at dusk and in the early evening hours. This was done to minimize disturbances on the *Galea* colony which was located near a footpath used during the day by farmers. I observed *Kerodon* and *Galea* in both the field and in the colony for over a year before beginning the time budget observations. In the wild, *Kerodon* and *Galea* were active throughout the day, with peaks in activity during the crepuscular hours. Both genera were active 24 h a day in the colony, with a depression in the level of activity during the mid-afternoon. Although these observations were not quantified to the degree the time budgets were, I observed no qualitative differences in the kind and frequency of activities exhibited during either the early morning or the late afternoon activity peaks. Animals were fed once daily, and the hour of feeding was set so that time budgets were calculated for both species approximately 12 h after the addition of food. This was done to eliminate possible differences in the allocation of time that might have occurred if the animals were at different levels of satiation.

For each time budget, a single animal was observed intensively for 0.5 h. The determination of which animals would be observed was random. Each animal was observed from between one to four times, giving a total of 56 *Kerodon* trials and 24 *Galea* trials. All movements of the animal were described and recorded on cassette tape. After the observations, the tape was played back, and the time spent in each behavioral category was marked by stopwatch and recorded in 3-min intervals, so that each individual data sheet contains what is essentially "a complete record" of the behavior for each animal observed, allowing for the analysis of both frequencies and durations of all events, as well as sequence analysis of series of events (Slater, 1978).

Data Analysis

Multivariate techniques have been used primarily for the examination of morphological (Blackith and Reyment, 1971) or morphoecological (Karr and James, 1975; Mares, 1975, 1976, 1980; Cody, 1978) traits. Recently multivariate techniques also have been applied to behavioral data (Svendsen and Armitage, 1973; Bekoff et al., 1975; Hazlett, 1977; Colgan, 1978; Davies, 1978; Ringo and Hodosh, 1978). Two techniques, which are of particular value to the ethologist, are principal components analysis and discriminant analysis. The basic methodology of these analyses and their application to behavioral data have been described in detail by various authors (Cooley and Lohnes, 1971; Aspey and Blankenship, 1977; Frey and Pimentel, 1978; Pimentel and Frey, 1978; Lacher, 1980).

A few precautions about statistical inference with these analyses need to be mentioned. Two basic assumptions of discriminant analysis are 1) group variance-covariance matrices are equal, and 2) all samples were drawn from a multivariate-normally distributed population. Although no program was available to test equality of the variance-covariance matrices, the large differences present among the within-group variances for certain

variables leads me to doubt that this assumption was met. As for the assumption of multivariate normality, Cooley and Lohnes (1971) stated that "we do not know of any useful test for multivariate normality."

I will assume that the above two assumptions have not been met and discriminant analyses (D.A.) will be treated as a descriptive heuristic process only. The only assumption necessary for the use of D.A. in this context is that all initial samples are potential members of the predefined populations (Neff and Smith, 1979). There is no difficulty in correctly classifying animals as *Kerodon* and *Galea*, or as males and females. Classification of animals as juveniles was based on external reproductive characteristics. No individual sample could potentially belong to a population other than those used in the construction of the discriminant axes.

When used as a descriptive process, discriminant analysis indicates the relative importance of the variables in separating the populations and indicates the relative distances between the centroids of each population. The influence of the inequality of variance-covariance matrices on classification of individuals is poorly known. Studies have shown that classification by *Geisser classification probabilities* performs well when the assumptions are not met (Pimentel and Frey, 1978). Geisser probabilities are more robust to departures from equality than are classification functions, the D.A. method employed in this study (SPSS DISCRIMINANT package; Nie et al., 1975). Discriminant analysis is, in general, especially robust, and has been shown to give close to optimal results even when variance-covariance matrices are significantly different (Lachenbruch, 1975; Neff and Smith, 1979). Thus probabilities of classification will be assumed to reflect the true biological affinities between samples and populations.

Although discriminant analysis assists in the separation of these groups, it tells one very little about the nature of the variation within groups. This is best accomplished by the calculation of principal components for each of the homogeneous groups. The computation of principal components requires no assumptions about the structure of the data, as long as no statistical inferences are to be drawn (Neff and Smith, 1979).

The ability to use quantified aspects of an animal's ethogram as a "system of measurement" in order to compare closely-related species is especially appealing to the ethologist. In this study, all recorded aspects of the behavioral repertoire of each species as well as certain acts which gave some indication of the importance of olfactory signals (sandbathing, scent-marking) were used in the quantitative analyses (Table 1). A quantitative approach was chosen in order to facilitate the examination of species-specific differences by the criteria proposed by Eisenberg (1967).

The raw data used in the multivariate analyses were taken from the time budget sheets. Both number of occurrences for each trait and total time spent in each behavioral act were recorded, but mean duration was chosen as the variable form to be analyzed. Duration is widely used in behavioral research, as it gives an estimate of the degree of variability or stereotypy of behavioral acts. It also has advantages over both frequency of behavioral acts and total time spent in the various behaviors (Bekoff, 1977; Fagen and Young, 1978). Mean duration is the only variable form which allows the observer to treat all behaviors as a unit phenomenon possessing a variable temporal component.

Mean durations were calculated from the time budget data for

all displays observed. For each trial the total time an animal was observed performing a given behavioral act was divided by the total number of times the act was performed. Each 0.5-h trial presents mean durations for all aspects of the behavioral repertoire executed during the observations. Displays not executed during a given trial were, by definition, of zero duration. Each trial was considered one sample unit. The total sample size for each group on which time budget data were collected was therefore equal to the number of trials performed on animals of that group.

Durations have been used as a behavioral phenotype in a variety of comparative studies (see Bekoff, 1977, for a review), particularly to compare mean durations and their coefficients of variation. Although the same is being done for *Kerodon* and *Galea* (Lacher and Mares, in preparation), the objective in these analyses was to determine if a population could be defined in terms of the mean durations of the various displays present in the behavioral repertoire. In addition, I wished to determine how consistently a given animal could be correctly classified into a population, based on a single observation period for which mean durations were calculated.

One inherent difficulty was related to the degree of commonness of certain acts. Not all acts were observed in a single observation period. This especially created difficulties when attempting to compare populations.

For example, a given display may have exactly the same mean duration in three different populations, however, may occur in quite different frequencies in each. Referring to Eisenberg (1967) the above discrete behavior patterns exhibited a profound similarity in duration. A simple comparison of durations, however, neglects a second important concept which is invaluable in any attempt at classification: "differences in the frequency of occurrence, rather than in the form (or mean duration, in this case) of the movement have proven to be the most effective criteria for delineating taxon-specific differences" (Eisenberg, 1967).

I therefore weighted all measurements of mean duration for a given population by the frequency of occurrence within that group. Mean population-durations for all displays in the behavioral repertoire (Table 1) were calculated by summing the mean durations for all the trials, and dividing by the total number of trials in that population. Mean durations of zero were thus included in the calculations. Individual cases (each 0.5-h trial) were then assigned a probability of classification within each population, based upon the comparison of the suite of mean durations with the corresponding mean population-durations of each group.

The analysis of durations may reveal additional information of biological relevance. In a discussion of behavioral act durations, Fagan and Young (1978) note that there are two possible types of behavioral acts. One type of act has a termination point which is independent of the time at which the act begins (that is, interrupted by another). Such acts exhibit a negative exponential probability distribution. A second type of act tends to terminate with increasing probability as the performance time increases. Their performance will begin when the benefit resulting from the act outweighs the cost of its enactment, and will end when the cost exceeds the benefit. This kind of act would represent what the ethologist commonly refers to as a behavioral display (for example, the relatively uniform postures and movements discussed by Eisenberg, 1967, in his report on comparative rodent behavior). The coefficient of variation of the temporal duration of these acts would consequently be smaller than the

Table 1.—*The various categories of behavior used in the time budget analyses. There are four functional groupings of acts, each of which contains a number of variables. A number of relatively infrequently observed acts that were not recorded during the time-budgets are not included.*

Maintenance and locomotion
a) Inactive (out of sight in rocks)
b) Sitting, rocks
d) Sitting, ground
d) Sitting, tree
e) Sitting, sand
f) Running
g) Climbing
h) Walking
i) Sandbathing
j) Grooming
k) Suckling
l) Nursing
m) Foraging/drinking
Aggression
a) Lunging
b) Chasing
c) Fleeing
d) Grappling
e) Curved-body posture
f) Submit
Reproduction
a) Follow (Chin-rump)
b) Followed
c) Tail-up
d) Repulsed
e) Mounting
Contact-promoting behavior
a) Crawl-overs
b) Allogrooming
c) Scentmarking
Estimate of degree of activity
a) Activity-ratio

coefficient of variation for "interrupted" act durations. One type of act would therefore exhibit a fairly limited temporal variability (that is, stereotypy), whereas the other type would exhibit the opposite property (that is, variability).

Using these criteria, it is possible to construct classes of behavior that can be separated by appropriate statistical analyses (Table 2). In this framework, Class I behaviors are those which are important in separating groups (for example, species or sexes). Class II behaviors are those that are of little importance in group separation, but which indicate acts that are important in maintaining higher-order group integrity (for example, acts shared at the generic level in an interspecific analysis). Class III behaviors are those that function as "interrupted-behaviors" (that is, behavioral acts which are *not* duration specific and occupy random length time periods that are disrupted at variable intervals by other acts or displays). Class III behaviors may also have an importance which is not related to duration, thus they should be cautiously interpreted.

Table 2.—The classes of behavior, based on stereotypy and variability. Once groups are defined, the three behavioral classes can be distinguished through discriminant analysis and the examination of coefficients of variation. See text for a more detailed description.

Class	Type of variability	Level
I	Low intragroup variability High intergroup variability	Group-specific behaviors
II	Low intragroup variability Low intergroup variability	Behaviors common to higher group levels
III	High intragroup variability High intergroup variability	“Filler-behaviors” or not duration specific

Discriminant analysis proved to be of particular value in distinguishing behavioral acts by these criteria. Variables, which were indicated as differing significantly between groups by discriminant analysis, were subsequently analyzed by a variety of univariate tests (Table 3). Once groups were defined, factors, which were important in explaining significant percentages of the intragroup variance, were constructed by a principal components analysis.

Field Studies

Population and reproductive data were collected simultaneously for both *Kerodon* and *Galea*, which were sympatric at the study site. Animals were live-trapped for a one-year period beginning in October 1976. In addition, *Kerodon* were handicapped and marked beginning in January 1978 until April of the same year.

For live-trapping and observations of movements, the study area was divided into six subdivisions. Each subdivision contained a major rock pile, and was trapped for a minimum period of 8 days. The traps were then rotated to another subdivision. In place of a grid, traps were placed in an irregular pattern throughout the site. Because of its physiognomy, the site was difficult to accurately grid. Piles of large boulders (3 to 6 m high) were separated by crevasses, vine tangles and thorny vegetation. A second disadvantage of a grid was related to the daily movements of the animals. *Galea* extensively utilize well-marked runways, and a regular grid would have potentially missed many

runways. *Kerodon* are extremely habit specific, being associated with the boulder piles, which were located throughout the study area, and a grid would therefore have placed too few traps in *Kerodon* habitat. I thus chose to place traps selectively on runways and in rockpiles to increase trapping and marking success of the animals. Intertrap distances were then measured to calculate home range sizes.

Trapped animals were weighed, sexed, and checked for reproductive status. All new animals were toe-clipped for future identification. In addition, all *Kerodon* were marked with a commercial fur dye, Jamar D, for easy individual recognition in the field. Observations of these marked animals were used to supplement the trapping data on home range and movements.

As *Kerodon* proved to be extremely difficult to trap, beginning in January of 1978, the animals were captured with the assistance of dogs and a number of young children. *Kerodon* were cornered in the rocks by the dogs, and subsequently captured with nooses by the children. These animals were weighed, sexed, toe-clipped and dyed, and their subsequent movements followed visually. These observations on movement were taken from a series of points on the study area, an equal amount of time being spent at each point.

General behavioral observations in the field were concentrated at two particular localities on the site (III and VI in Fig. 3), although observations were taken on various occasions throughout the study site. Observations were made either from behind a blind or in the shelter of some vegetation. Watch periods varied both in length (30 min to 3 h) and in the time of day observations

Table 3.—A summary of all statistical procedures used, indicating the source, and the groups compared. Additional procedures used for special situations are not included, and are referenced in the text when applied.

Test	Source	Groups compared
Mann-Whitney U-test	BMDP3S (Dixon, 1975) Siegal (1956)	<i>Kerodon</i> sexes <i>Galea</i> sexes
One-way F-test	SPSS ONEWAY (Nie et al., 1975) Sokal and Rohlf (1969)	All groups All adults
Kruskal-Wallis test	BMDP3S (Dixon, 1975) Siegal (1956)	All groups All adults
Non-parametric multiple comparisons	Hollander and Wolfe (1973)	All groups All adults
Discriminant analysis	SPSS DISCRIMINANT (Nie et al., 1975) Pimental and Frey (1978)	All groups All adults
Principal component analysis	BMDP4M (Dixon, 1975) Frey and Pimental (1978)	All <i>Galea</i> Adults <i>Kerodon</i> males <i>Kerodon</i> females

occurred (ranging from dawn to dusk), with emphasis during crepuscular hours. All field observations were compared to observations made in the more controlled colony situation in order to evaluate possible differences that may have existed.

The total observation time, for both field and colony studies, was approximately 1,600 h. In the following descriptions of the behavioral repertoires, I use the terms "display" and "gesture" as synonyms.

RESULTS

HABITAT ANALYSIS

The record of maximum temperatures shows a cycle with high temperatures September through December, followed by a cooling trend (Fig. 5). The temperature remains low until mid-July, when it again climbs to the September levels. The minimum temperatures follow the same trend, but tend to lag behind the maximum temperatures. The coolest temperatures of the year coincided with the period of the most regular rainfall, late April through August. These months are generally considered the rainy season in the Exu area, but during the year that these data were collected there was no well defined rainy season, and rain occurred periodically throughout the year. Conversations with local farmers and the Serviço de Peste in Exu indicated that 1976–1977 was an especially wet year. Indeed, with the exception of a few species, there was no period of deciduousness that year; vegetation is usually sparse during the dry season in the Caatinga.

Although the study site was a relatively small area, the high structural diversity present allowed for a fairly high species richness of plants (Table 4); 29 families, 55 genera, and 70 species are represented. There are a number of different microhabitats present that tend to be dominated by one or a few species. The relatively level, rock-free areas were dominated by low canopy second growth thickets of *Croton jacobinensis*, *Cordia globosa*, and, in areas where the soil became somewhat rocky, *Croton argyrphylloides*. More recently cut level areas were dominated by various species of Malvaceae (*Bogenhardia tiubae*, *Sida paniculata*), Compositae (*Centratherum punctatum*, *Blainvillea rhomboidea*), the vine-like Leguminosae (*Phaseolus* and *Macroptilium*), and, on the more open areas, various grasses (Gramineae, Cyperaceae).

Cacti, especially the two species of *Pilosocereus*, were most common in the boulder areas. The common trees were *Cordia insignis* and *Cedrela* sp., and occasionally *Erythroxylum* and *Rhamnidium*. A heavy vine layer of *Cissus simsiana*, *Cissus sicyoides*, *Serjania caracasana*, *Serjania* sp., and

Vismia guianensis blanketed the trees and low vegetation. In addition to the above three habitats, which were the most extensive, there were three additional areas of relatively uniform vegetation on

Table 4.—Dates of the first observation of selected traits and gestures in *Kerodon rupestris juveniles*. All values in days.

Trait	Individuals						
	J2	JR	JF	J5	B1	B2	B3
<i>Maintenance and locomotion</i>							
Frisky-hops		2	13				
Running	7	2	7		3	3	
Climbing	14	9			21		
Basking	14	36					
Stretching		14					
Yawning		14					
Grooming	14	6			29	2	3
Refection		6			29		
Foraging	14	17		12	7	13	3
Drinking		15					51
<i>Aggression</i>							
Lunge		45		101	48	28	
Chase	28			34			51
Flee	98	15	12	21	32	58	51
Grappling	70	15				26	26
Grappling stops	175	80		57	54	71	71
Submit		76					51
<i>Reproduction</i>							
Follow	84			105			
Followed		17	12		30		
Circling	210						
Mounting	70	30		34			
Copulation	84						
Estrous		71			60		
Copulatory Plug		83					
Pregnancy		81					
Partum		156					
Testes down	119			113		114	114
<i>Contactual behavior</i>							
Crawl-overs	14	3	9		4	2	2
Allogrooming	70		12				
Nose-nose					46	51	
<i>Vocalizations</i>							
Alarm call	84	2					
<i>Weaning</i>							
	35	48		35	23	25	45

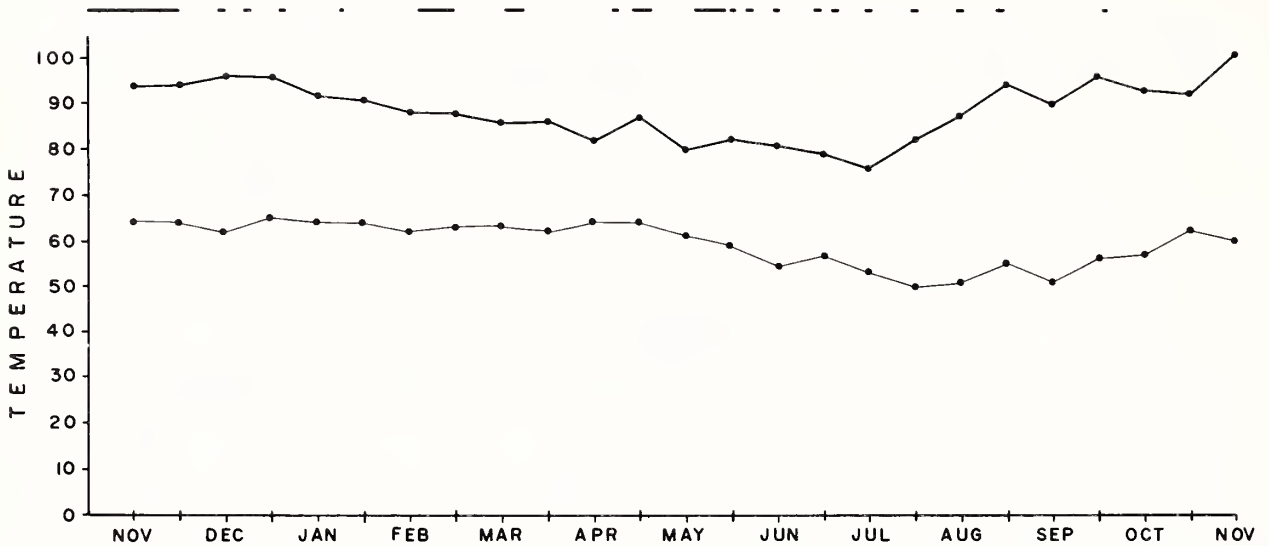


Fig. 5.—Weather data collected at the Fazenda Batente study site for November 1976 to November 1977. Dashed lines above the graph indicate days with rainfall. Upper graph represents 15 day maxima and lower graph 15 day minima in degrees Fahrenheit.

the study site. One area had been previously cultivated, and was still dominated by the domesticated fruit-bearing plants *Mamordica charantia*, *Cucumis anguria*, *Lycopersicon esculentum*, and *Solanum americanum*. A small rocky area between two large boulder piles was almost entirely occupied by *Cnidocolum urens*. A third locale, which was a flat sandy area separating the study site from an adjacent stream bank, primarily contained the shrubs *Jacobinia* sp. and *Ruellia asperula*, with a mixed grass ground cover. This area was separated from the stream bank by a line of trees of *Cassia excelsa* and *Pterogyne nitens*.

Although no statistical technique of habitat analysis was used to define the above six microhabitats, the combination of structural and floristic differences that existed made each area quite easily distinguishable from the others. Trap sites could therefore be assigned to a given microhabitat with confidence.

MAINTENANCE BEHAVIOR

Ingestive Behavior

Feeding.—Although foraging behavior is basically the same in both genera, there were a number of notable differences. *Galea* walked with the body held close to the ground, the head also held low and extended forward. The animals proceeded forward interspersing slow, cautious steps with series of quick hops. They would periodically hold the head high, looking around and sniffing the air. *Galea*

rarely manipulated food with the forepaws. *Kerodon* also moved forward with the same low-body posture, holding the nose just slightly above the level of the ground (Fig. 6c). Like *Galea*, they also interchanged bouts of slow walking and hop-like running while exploring. When *Kerodon* paused, they generally sat upright, with their front paws off the ground, very similar to a dog begging (Fig. 6a, b). While in this position, they sniff the air and look around. *Kerodon* in the field, however, spent very little time foraging on the ground, and when they did, it was almost always on a rock surface. The majority of foraging bouts observed in the field occurred in trees. Animals would emerge from rock fissures and move about on the tops of boulders. From there they would climb into adjacent trees and forage on leaves, buds, flowers, and bark. When disturbed, animals would leap from the trees, breaking their fall by grasping at branches and vines on the way down. *Kerodon* used the forepaws extensively while foraging, commonly sitting upright and holding a leaf in both hands while eating. In the field, both genera foraged day and night.

Drinking.—Animals were only observed drinking in the colony. Both genera lean over the water source (dish or puddle) and lap the water without raising the head. Animals would occasionally pause and look about, then continue drinking.

Refecation.—Both genera were observed nibbling the anal region, then lifting the head and chewing (Fig. 10a).

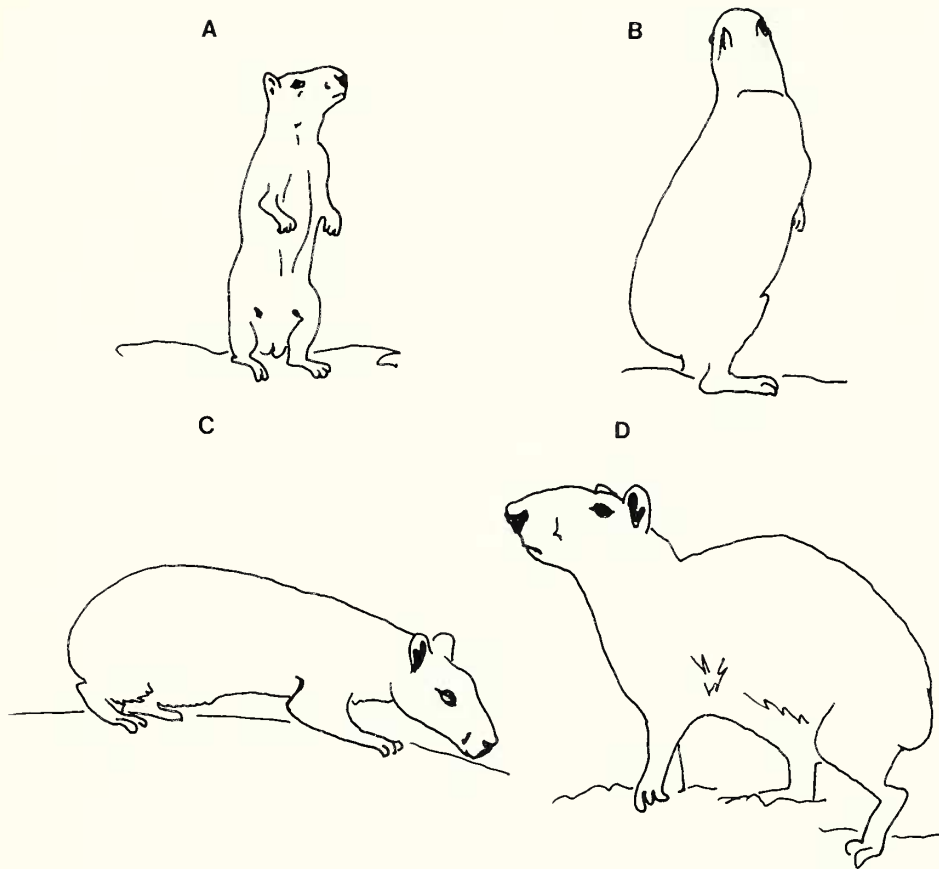


Fig. 6.—Upright exploratory postures (a and b), foraging posture (c), and attend position (d) of *Kerodon*.

Locomotion

Walking and running.—Both *Kerodon* and *Galea* walk quadrupedally with alternating steps. Walking was most commonly observed while animals were casually feeding. Animals would also accelerate into a run, using the same alternate foot pattern, although rapid locomotion more often consists of series of hops. During aggressive chases and when following a female, *Galea* would often exhibit a bounding locomotion (stotting), similar to *Dolichotis* (Dubost and Genest, 1974). When hop-running, *Kerodon* sprung simultaneously off its hind-feet, then alternated the left and right forepaws, then sprung off the hind feet, and so on. *Kerodon* are extremely agile while running in the rock piles, and would often run full speed towards a rock, leap against the surface, then twist the body up to 180° while in the air, running in a completely different direction upon landing. They possess considerable spring in their hind limbs, and can easily leap from a run up onto a 3-ft high boulder. At times (for

example, exploring a strange area) they would run short distances in quick bursts, then stop and reorient their body in jerky 90° and 180° turns.

Climbing.—Although Rood (1972) reported climbing behavior in *Galea musteloides*, *Galea spixii* were never observed climbing. *Kerodon*, however, were extremely agile climbers (Fig. 7). When ascending a tree, *Kerodon* used an alternating foot pattern much like a man climbing a ladder. Once in the tree, *Kerodon* moved along the branches with the body held close to the branch, again using a left forepaw, right hindfoot, right forepaw, left hindfoot pattern. For animals of their relatively large bulk, *Kerodon* were capable of navigating extremely delicate branches, and were observed moving about in the field and in the colony on branches of less than 1 cm in diameter. When moving from branch to branch, they generally reached out with the forepaws, secured the branch, and then stepped or hopped over with the hindfeet. When descending, *Kerodon* either stepped down, as if descending a



Fig. 7.—*Kerodon* adult sitting on a low branch shortly after emerging from the rocks.

ladder headfirst, or slid down backwards or sideways. When frightened, they would leap 10 to 20 ft to the ground, breaking their fall by grasping at branches during the descent.

Frisky hops.—Both *Kerodon* and *Galea* juveniles exhibited frisky hops. The animal would leap into the air, twist the body and shake the head to and fro, often landing in a different orientation. Frisky hops were occasionally accompanied by bouts of exaggerated running. The various components present in frisky hops correspond quite closely to the components of Locomotor-Rotational movements described in Wilson and Kleiman (1974). The importance of olfactory stimulation in eliciting frisky hops, however, has not been defined.

Resting Posture

Galea spixii resting postures were the same as described for *G. musteloides* (Rood, 1972). *Galea*

would commonly form a small nestlike depression in the dry grass in which to sit (Fig. 8). *Kerodon* exhibited a variety of resting postures (Fig. 9). There were two basic sitting postures—one in which the animal maintained the forelegs erect, with the chest off the ground and the head up; and a second more relaxed posture with the venter in contact with the substrate, the forelimbs bent, and the head drooped with the eyes partly closed. Animals were commonly observed in the latter position sitting in the sun. *Kerodon* would often shift from this second sitting position to a semiprostrate posture, with both hindlegs extended out to one side. In very hot weather, *Kerodon* would lie flat on the ground with the hindlegs splayed out behind. A common gesture in both *Kerodon* and *Galea* as they sat was the head twitch, a rapid shaking of the head, tilted to one side. Its apparent function was to shoo small flies and mosquitoes away from the eyes and ears.



Fig. 8.—Adult *Galea* in typical resting posture.

Grooming

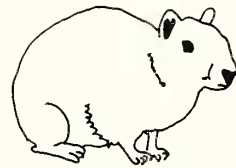
Face wipes.—These were exhibited in both genera (Figs. 10b, c; Fig. 11; Fig. 12a). The animal licked the forepaws, either together or separately, then using the inner side of the paws, wiped the face from behind the ears to the nose. The cheek areas were wiped most often. Both paws were used simultaneously, alternately, or one at a time. *Galea* generally sat on their haunches while face wiping, whereas *Kerodon* more commonly sat in a “begging dog” posture.

Scratching.—Both genera used the hindfeet to scratch the ventrum, side, back, and head, particularly behind the ear. *Kerodon* possesses a grooming claw on the innermost digit of the hind foot, which it used to groom the pelage (Fig. 12b). The mouth was often used to clean the claws after scratching.

Nibbling and licking.—Both genera nibbled the fur with the incisors. The areas groomed included all areas posterior to and including the shoulders and forelimbs. In addition to licking the paws during face wipes, animals were observed to lick the anal and genital regions. Adult females would often lick the anal region of young juveniles, apparently to stimulate defecation.

Nosing.—Both genera also groom by rubbing the nose through the fur of the sides and belly.

A



B



Fig. 9.—Typical sitting posture of *Kerodon* adult (a) and juvenile (b).

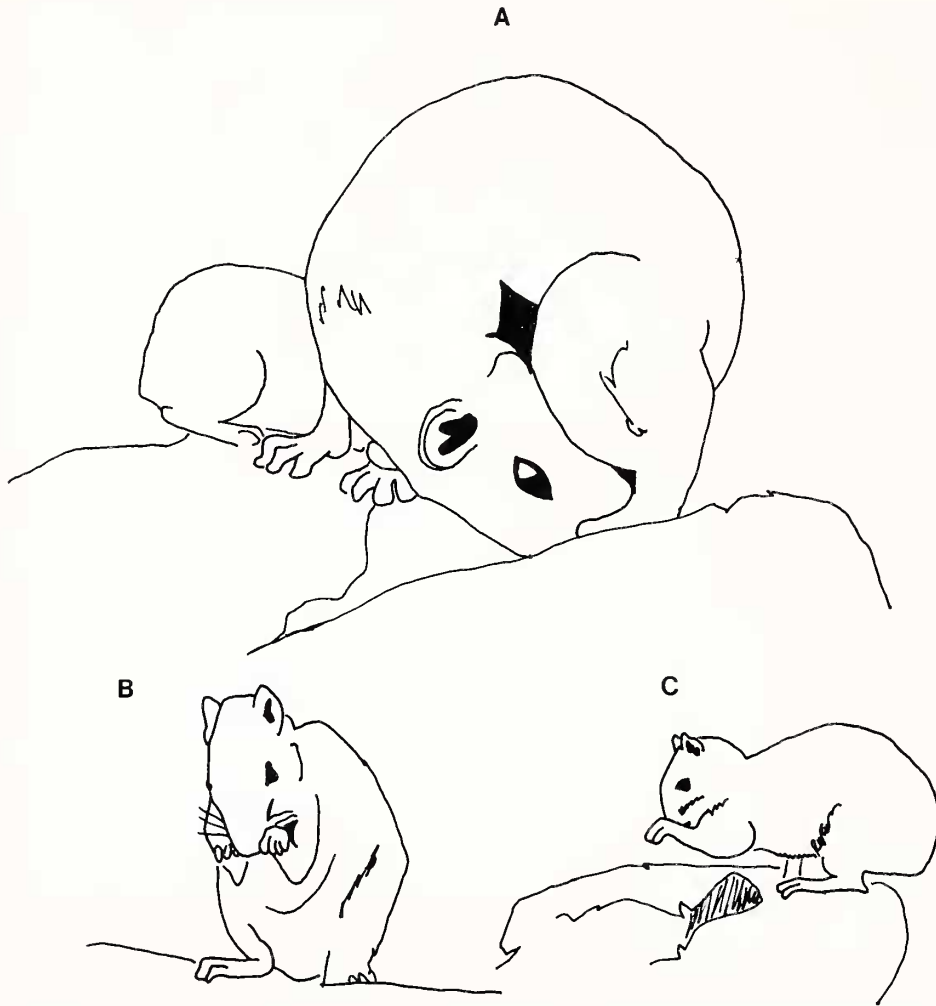


Fig. 10.—Adult *Kerodon* exhibiting refection (a) and two different postures of an adult grooming by face wipes (b and c).

Combing.—When nosing the pelage, *Kerodon* would often sit upright, and simultaneously comb the fur with the forepaws. As in nosing, the sides and ventrum were combed. *Galea* were not observed combing.

Rolling and sandbathing.—This aspect of grooming behavior was observed only in *Galea*, and formed an integral part of this species' sandbathing behavior. *Kerodon*, although provided with sandbathing arenas, did not sandbathe. There were two basic components to sandbathing in *Galea*—side rubs, during which the animal would roll onto its side, generally in a sandy or dusty area, and vigorously kick backwards with both hindfeet; and ventral rubs, in which the forelimbs were held under the body, the belly was flat against the substrate, and the hindlimbs were again vigorously

kicked backwards. When siderubbing, the forelimbs and chest were usually in contact with the ground, but occasionally the animal would roll completely onto its back. In addition, animals frequently reoriented their body position during ventral rubs, kicking a few times, then turning 180° (that is, head now in rump position), and kicking again. This sequence was often repeated several times. As rolling and sandbathing were highly integrated with marking behavior, they will be discussed further in the next section.

Marking

Kerodon in the colony were observed dragging the perineum, and apparently marking, only three times in 20 months of observation. This behavior was not seen in the field. This indicates that olfac-



Fig. 11.—Adult female *Kerodon* face wiping.

tory communication may not be as important in *Kerodon* as in *Galea*, a species which exhibits frequent scentmarking behavior. *Galea* scentmarking occurred both separately and in conjunction with sandbathing. Marking during sandbathing occurred primarily during ventral rubs, when the animal would drag the perineum forward in between kicks. Occasionally the animal would pause in the ventral rub position and rub the perineum from side to side, then continue sandbathing. *Galea* were also observed to urinate while performing a perineal drag.

Sandbathing and marking were observed in a variety of situations. All animals marked and sandbathed intensively upon introduction to the colony. When a strange male was introduced to the already extant colony, he urinated, marked, and sandbathed extensively within 3 min after his introduction. On one occasion the dominant male was observed to scentmark and sandbathe on the same spot where a subordinate male had done the same a few minutes before. Marking was also observed in more specific aggressive situations. The dominant male was observed marking after chasing a subordinate,

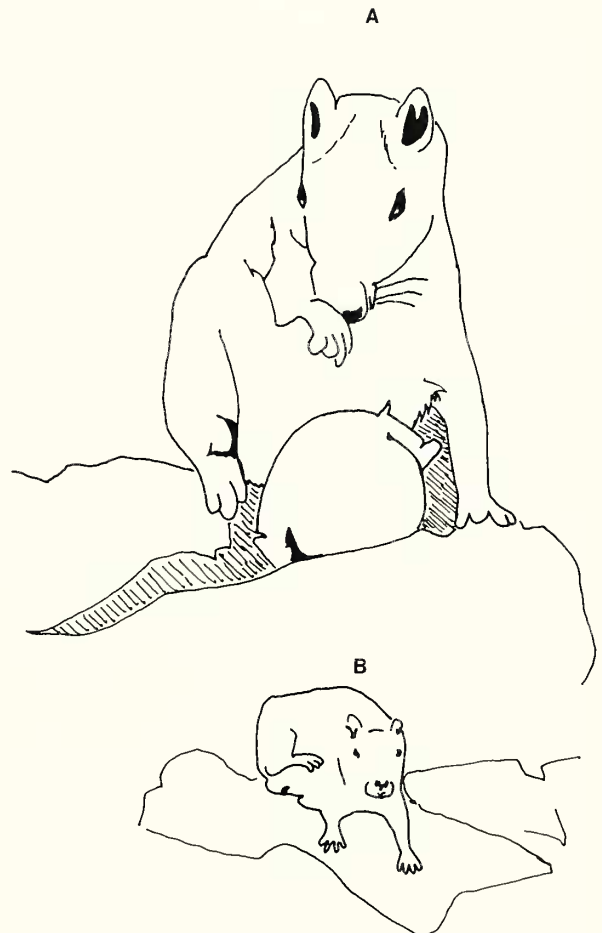


Fig. 12.—Adult female *Kerodon* face wiping while a juvenile nurses (a), and an animal grooming the head and neck with the hind-toe grooming claw (b).



Fig. 13.—Juvenile *Kerodon* suckling from the forward position.

and the same behavior was also observed in the dominant female. The spot marked was the point at which the chased animal had initially been sitting. In a reproductive context, a female was observed scentmarking after urinating on a male who was following her.

Comfort Movements

Both genera often stretched and yawned while resting. When stretching, they would commonly stretch the body, then stretch one hind leg out behind, followed by the other. *Kerodon* was observed stretching the hindlimbs by kicking back in a manner very similar to that employed by *Galea* while sandbathing. The strong correspondence between the postures and movements suggests that such comfort movements as stretching may be the origin of more complicated series of movements such as those used in sandbathing. Within *Galea*, the movements used while stretching are essentially sandbathing movements in slow motion.

Digging

Digging was not observed in either *Kerodon* or *Galea*.

Elimination

When urinating, both genera would elevate the hindquarters slightly. *Kerodon* also would occa-

sionally lift one hindleg and extend it to the side. In the field, *Galea* feces were generally encountered in runways. *Kerodon*, however, defecated in a number of selected areas in each rockpile. Great quantities of feces would accumulate in these areas, in piles 1 to 3 ft in diameter and often an inch or two deep. This same behavior is exhibited by another group of rock dwelling animals, the rock hyraxes (Hoeck, 1975).

Attend

In response to an external stimulus, *Galea* would sit upright, forelimbs extended, with the head raised. The animal would freeze in this position, and would subsequently flee for cover or resume its earlier activity, depending upon the presence or absence of subsequent stimuli. The dominant male was commonly observed in an attend position, apparently observing the movements of other animals. He would generally sit on top of a large rock while in this position to facilitate his observations. *Kerodon* normally sat in a relaxed posture, hunched slightly forward. As birds moved or called in the forest, *Kerodon* occasionally watched them, but didn't change posture. When an unexpected rustling occurred in the trees, the animal would move its body forward onto its toes, extend the forelimbs, and stretch its upper body and head forward (Fig. 6d). If the stimulus were sufficiently intense, *Ker-*



Fig. 14.—Two views of nursing postures in *Kerodon* (a and b).

odon would abruptly turn towards the adjacent crevice and ready itself for fleeing. When in this position, animals would commonly raise one foot up and sniff at the air. They would occasionally go into a complete upright posture. In addition, the animal often made rapid 90 and 180 degree pivots of the body while in the attend position maintaining the rump at the same point. *Kerodon* alarm whistles were usually given from an attend position.

SOCIAL BEHAVIOR

Contactual Patterns

Nursing postures.—*Galea* females generally sat in an attend-like posture while nursing; occasionally adult females would lie down and close their eyes. Juveniles would generally suckle from the side; at times they would suckle from in between the forelimbs of the female. When two juveniles were being

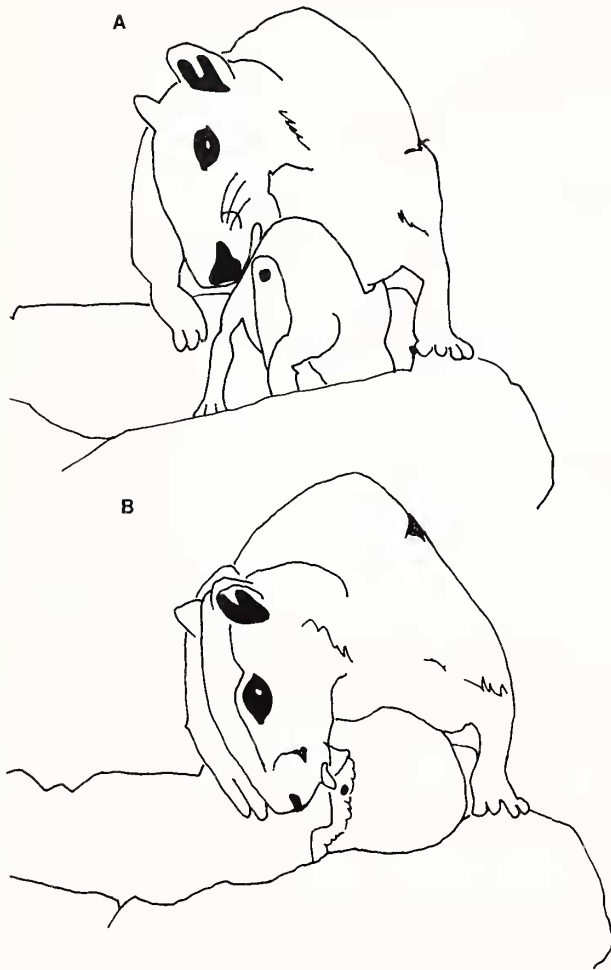


Fig. 15.—Adult female *Kerodon* grooming a suckling juvenile—licking fur (a) and anogenital region (b).

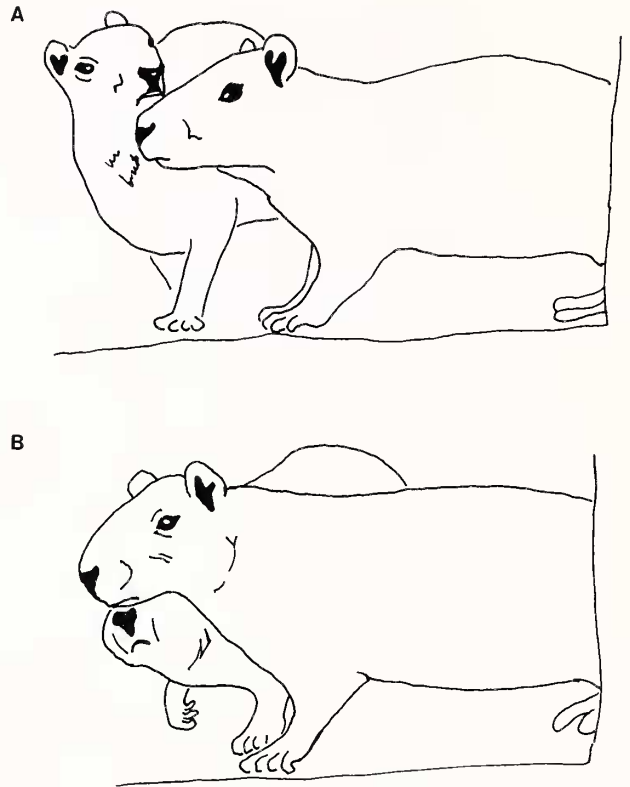


Fig. 16.—Two face-face contact positions in *Kerodon*—chin-on-nose (a) and sniffing facial region (b).

nursed, they would suckle on the posterior pair of teats from different sides or from the same side of the body. When three juveniles were suckling, they would utilize all four mammae. *Kerodon* females sat in a posture similar to *Galea* while nursing (Figs. 13, 14). Juveniles suckled both from the side and from the front. A juvenile would sometimes crawl completely under the belly of the female while suckling. When there were two juveniles, they suckled from the same side, or from different sides, and the teat order was not specific. Juveniles would occasionally pause while suckling and groom the face. The female would also groom herself while nursing, and at times would groom the juveniles (Fig. 15). Before juveniles began suckling, they often performed a series of climb-overs on the back of the female. After a number of climb-overs, the

female then allowed the juvenile to suckle. Females also occasionally rejected juveniles by shaking them from their backs, especially when the young animals were nearly weaned.

Social grooming.—This behavior was rare in *Galea*, and common in *Kerodon*. The only instance of allogrooming observed in *Galea* was an adult female grooming her juvenile. In *Kerodon*, however, there was a fairly complex network of allogrooming associations. The most common association was the grooming of juveniles by adult females, particularly while the young were suckling. Allogrooming between adult females, however, was never observed. This was in sharp contrast to the situation between adult males, where allogrooming was quite frequent. The animal most often groomed was the dominant male. He was generally groomed by subordinate males (numbers three and four in the hierarchy) who were his progeny or had been introduced to the colony as juveniles. The number two male, introduced as an adult together with the dominant male, never allogroomed another animal,



Fig. 17.—Two adult *Kerodon* exchanging the nose-nose recognition gesture.

although he was himself allogroomed by the number four male. The number three and four males once allogroomed each other before their respective orders in the hierarchy had been clearly established. Intersexual allogrooming was infrequent. An adult female once groomed the dominant male and attempted to groom the number three male, who lunged at her. The number three male allogroomed the dominant female once, and on a second occasion allogroomed an estrous female after an attempted mount. The areas allogroomed were predominantly the face, head, and neck, and occasionally the forelimbs and shoulders. The animal performing the grooming would either nibble or nose the pelage of the other. In the observed case of reciprocal allogrooming, the two animals placed their faces cheek to cheek, and nibbled at each others neck and ear regions.

Nose-nose and kiss.—Face-face contact was used as an apparent recognition gesture in both genera (Figs. 16, 17). Initial nose-nose contact in *Kerodon* was sometimes followed by the cheek to cheek gesture described in social grooming, as well as a general sniffing of the body (Figs. 18, 19). In addition, one animal would at times place its chin on the back of the other following a nose-nose gesture (Fig. 19a). A gesture resembling the kiss described by Rood (1972) for *Microcavia* was also

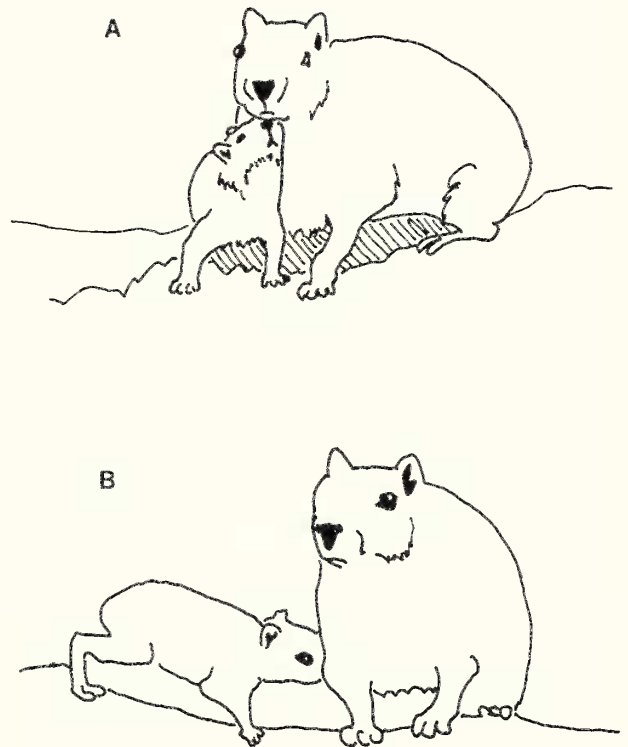


Fig. 18.—Juvenile *Kerodon* nuzzling face (a) and side (b) of adult female.

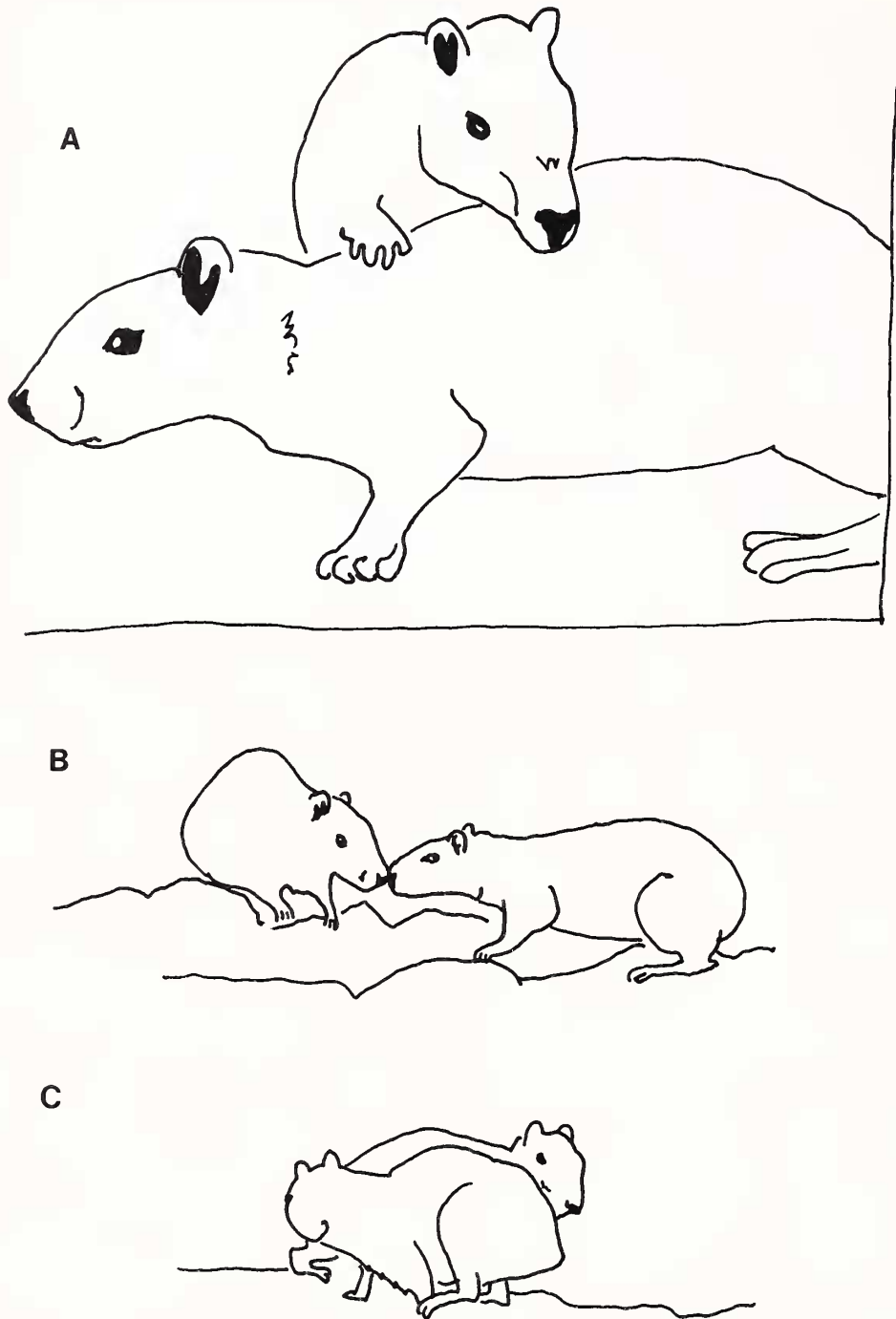


Fig. 19.—Contact-promoting behavior in *Kerodon*: chin on back (a), nose-nose (b), and mutual naso-anal (c).

observed in *Kerodon*, a mutual nuzzling of the mouth region.

Crawl-over.—This behavioral component was observed in both genera, though it was far more common in *Kerodon*. One adult female *Galea* had

a habit of following another adult female around the colony, and was observed crawling over the back of the female on several occasions. The following female also placed its chin on the back of the other. Adult females would also occasionally place the



Fig. 20.—Young juvenile *Kerodon* exhibiting crawl-over behavior on resting adult female.

chin on the back of a juvenile. In *Kerodon*, crawl-overs were observed in association with a variety of other gestures. Adult males were often observed either crawling-over, or resting their forelimbs, on the backs of females (Fig. 19a). Female-female crawl-overs were also observed, particularly in association with huddling. The chin-on-back gesture was also observed in *Kerodon*. Submissive males placed their chins on the back of the dominant male while allogrooming. Crawl-overs by males on females may actually be a component of sexual behavior, as males were twice observed exhibiting crawl-overs in association with other sexual behavior, like following and mounting. The most common situation in which crawling-over was observed was in adult-juvenile interactions. Juveniles would commonly crawl about on the backs of adults, particularly adult females (Fig. 20). A variety of positions was exhibited, including the chin on back. Juveniles would occasionally approach the adult from the rear and climb into a mounting-like position. Juveniles would also climb completely onto the back of a resting female. Adult females in return would at times place their chin on the back or rump of juveniles. Juvenile crawl-overs may have a function in stimulating nursing behavior in the adults (see Nursing Postures).

Grappling.—Grappling behavior was observed

only in *Kerodon* juveniles. Animals would rear up on their hind legs, grasp each other by the upper body and wrestle back and forth. While wrestling, the animals would often jump up and down, and when one animal would drop down on all fours, the other would climb or jump onto its back. Grappling was similar both to frisky hops and adult agonistic behavior, and is probably an important play behavior in the development of certain aggressive gestures. The actual aggressive counterpart in adults is jousting and jump-turns, which have the same basic structure, but are of a much higher intensity. A juvenile on one occasion attempted to grapple with an adult, who responded with an aggressive lunge. Grappling, in this case, elicited a true aggressive response from the adult. On another occasion an adult male was sexually following a juvenile, whose response at the male's approaches was to turn and grapple. The male gesture of attempting to mount served only to stimulate play behavior in the juvenile.

Huddling.—Both *Kerodon* and *Galea* were observed to rest in contactual positions while kept in cages. Animals rested in a variety of positions—side-side, head-over-side, rear-sit, and side-sit (Rood, 1972). However, in the large colony rooms animals generally rested in contact only when frightened or disturbed.

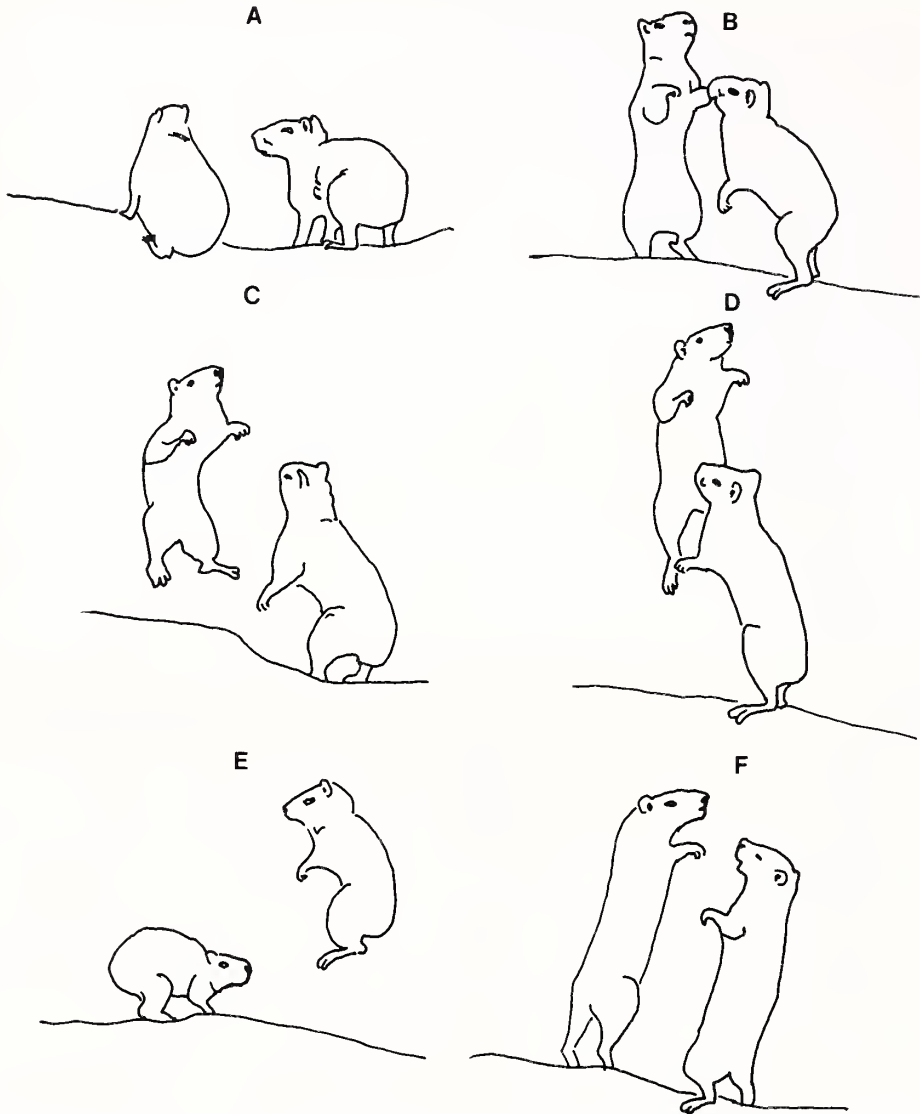


Fig. 21.—Agonistic behavior in *Kerodon*: Male on left in partial submit while male on right assumes threat posture (a). Males begin to joust (b and f) and jump-turn (c through e). The animal on the left in sketch (e) has been caught flat-footed during a series of jump-turns and has assumed a defensive posture.

Agonistic Patterns

Head thrust.—This was the lowest intensity aggressive gesture in both genera. The dominant animal would either jab the head forward or flick the head sideways in the direction of an opponent. In its most exaggerated form the aggressor would lunge its entire body forward, or in the case of a sideways thrust, would also throw its shoulders and forelimbs towards the submissive animal. Head thrusts did not appear to be associated with any specific type of encounter, but rather seemed to in-

dicate a fairly high superiority of the aggressor over the subordinate. It was the most common means employed by an adult to rid itself of a pestering or intruding juvenile. Dominant animals would often approach a subordinate individual in a fairly slow, deliberate walk with the head and shoulders held low and directed forward. The appearance of the body was thus much like the position assumed by the aggressive animal after a head thrust. The low body approach would often elicit a flee in a subordinate, the functional similarity likely being related to the structural similarity.

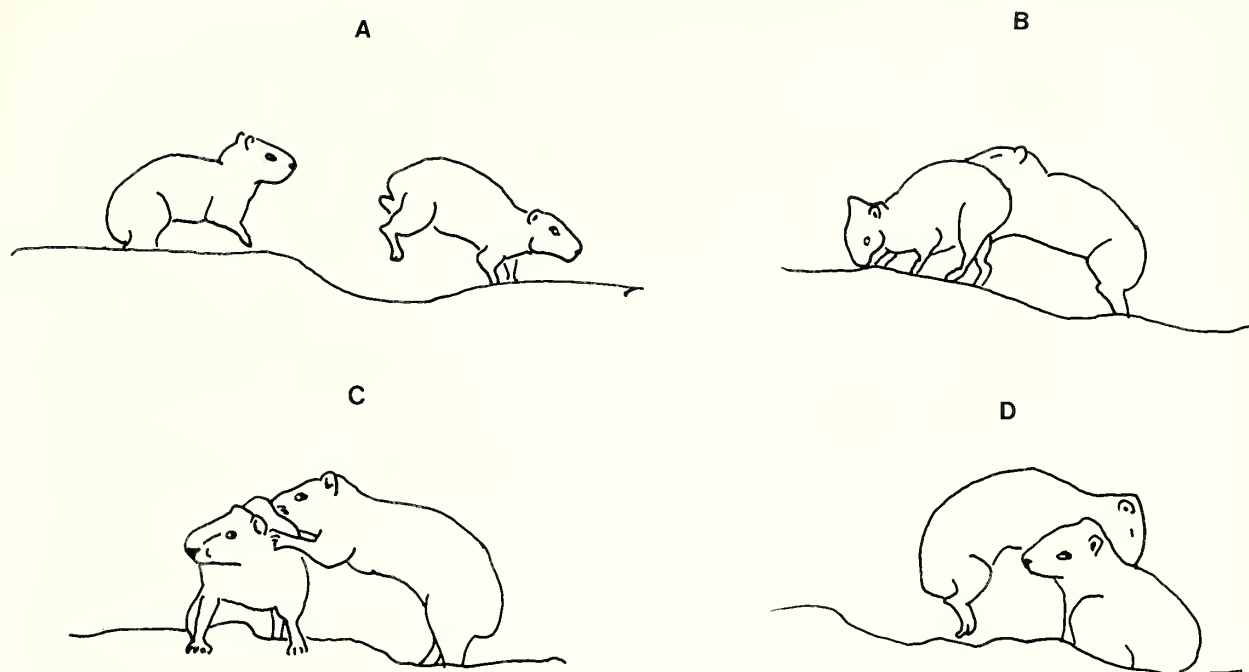


Fig. 22.—Agonistic behavior in *Kerodon*: aggressive chase (a), and three views of a dominant individual biting a submissive animal (b through d). The biting animal usually closes its eyes.

Attack lunge.—This act was also observed in both genera, and was essentially an exaggerated head thrust. The aggressor ran or jumped towards another animal, terminating in the head-thrust position. The final position varied slightly between the two genera. *Kerodon* attack lunges ended with the body held low and directed forward, and the head also directed forward and down. *Galea* terminated an attack lunge with the body directed forward; however, the forelimbs were usually erect and spread, and the head was angled forward and up, not down.

Chase.—If one of the above two gestures was not sufficient to instigate a flee from the subordinate animal, the dominant would then pursue the other animal in a running chase. The end result was generally that the submissive animal fled, and the dominant animal desisted. At times the chasing animal would actually pursue the subordinate until he caught it, and would attempt to bite the rump of the fleeing animal. *Kerodon* chases in the field were especially interesting, as the animals wove in and out of rock crevasses, and even climbed trees. The fleeing animal would often avoid an aggressor simply by crawling out onto a very thin branch.

Stand-threats.—*Galea* would frequently exhibit

curved-body postures in situations of unsettled dominance hierarchies. The two animals would characteristically slowly approach one another, then stop and stiffen their limbs, hunch the back, pull in the neck, and lower their heads. They would frequently exhibit piloerection. One or both animals would then lunge, and if neither fled, the animals would again assume a curved-body posture and continue the bout. When neither animal emerged victorious, they would maintain the curved-body posture for some time, then would mutually depart. Although *Kerodon* did not exhibit curved-body postures, they would, in between bouts of jousting and jump-turns (see below), space themselves parallel to one another, but facing in opposite directions, and slowly walk in large opposing semicircles. When walking, the animals would take peculiar deliberate, bobbing steps. An animal would also occasionally pause and rock the hindquarters to and fro. This particular gesture, which I termed *spacing and pacing*, was very uncommon. The act of aligning the bodies in parallel, but facing in opposite directions, seems to have its origin in the curved-body postures of *Galea* and *Cavia*.

Jump-turns.—Rood (1972) indicated that this trait was observed only in *Microcavia*; however, both

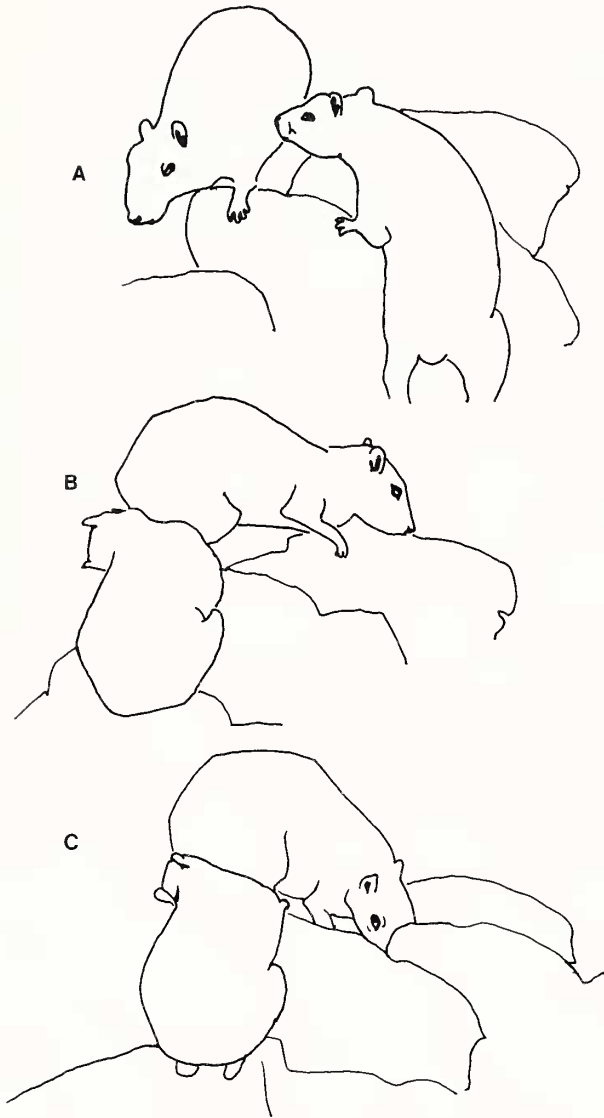


Fig. 23.—Sexual behavior in *Kerodon*: animal sniffs at sides (a) and ano-genital region (b and c) of female.

Kerodon and *Galea* exhibited jump-turns during colony and field observations. In *Galea*, jump-turns were most commonly observed during bouts of standthreats. One animal would lunge, and the other would jump into the air, both to avoid the lunge, and to attempt to grab onto its opponent's back. This animal would in turn jump-turn, also attempting to get "on top" of the other. Such an aggressive bout would generally consist of a rapid sequence of jump-turns, both animals attempting to gain the top position, and thus the advantage. The animal which gained the advantage would bite the rump and back of the animal on the bottom. The "loser" would

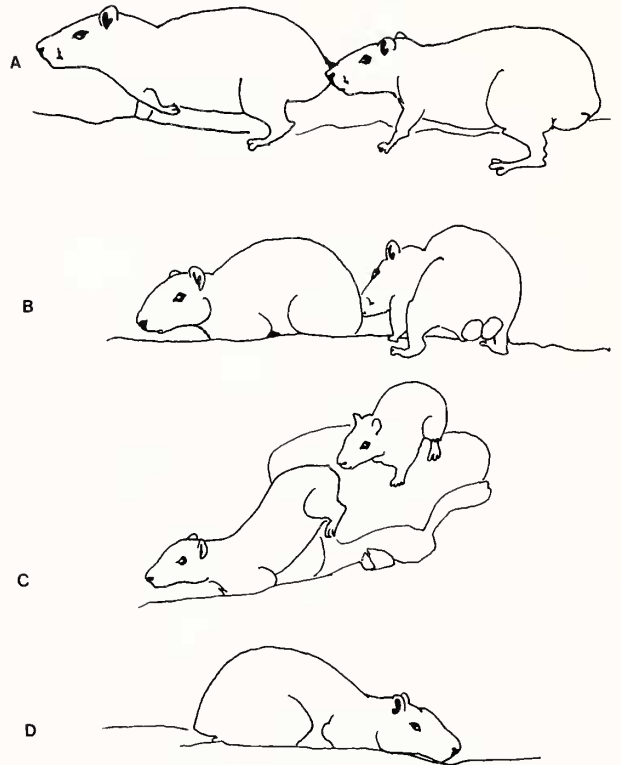


Fig. 24.—Sexual behavior in *Kerodon*: chin-rump follow (a), naso-anal by male while female depresses hindquarters (b), female tail-up (c), and adult female in full submit position in response to male advances (d).

then attempt to wrestle its way free, and would generally flee. At times neither animal would successfully dominate the other, and after a flurry of jump-turns the pair would segregate into curved-body postures, then begin the entire sequence again. Jump-turns in *Kerodon* also consisted of a series of jumps and twists during which one animal would attempt to get on top of the other (Fig. 21). They occurred most often in encounters of two "strangers," or of animals of approximately equal status in the hierarchy. They tended to be far more spectacular than *Galea* jump-turns, because of the great jumping ability of *Kerodon*. *Kerodon* jump-turns generally did not originate from a curved-body posture, but rather from an upright position. Animals would approach one another and rear up on their hindlegs. The two animals would then weave and bob on their hindlimbs, attempting to grasp one another by the upper body. This would then develop into an upright wrestling bout, termed *jousting* (Fig. 21). As *Galea* would alternate between curved-body postures and jump-turns, *Ker-*

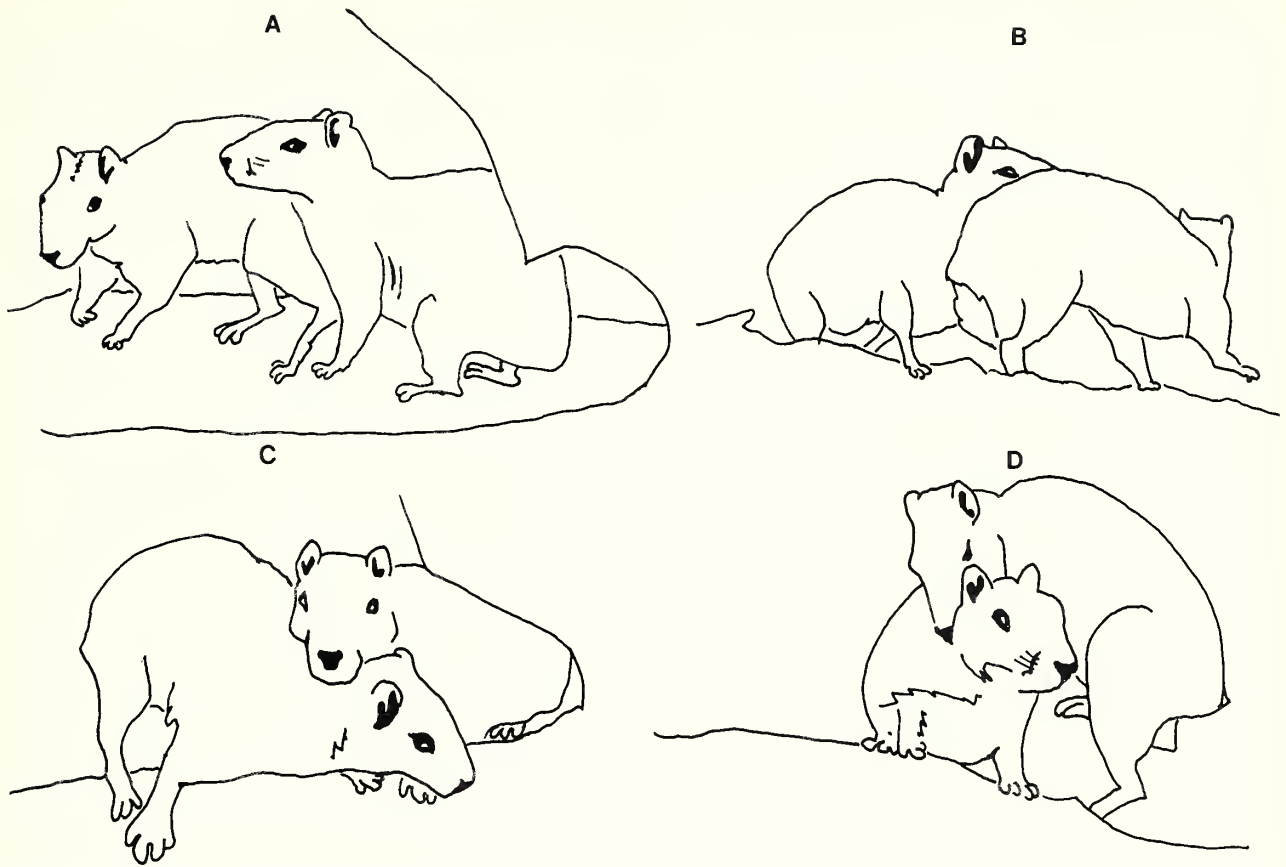


Fig. 25.—Four views of circling behavior in *Kerodon*. Adult male in front of adult female (a and b) stopping her forward advance. Male then passes under the chin of female (c) and swings around, securing female by the nape of the neck while attempting to mount (d).

odon would typically alternate jousting and jump-turns. In both cases, the winner was the animal which would pin the other on the ground, with the winner biting the back and rump of the loser (Fig. 22).

Retreat or flee.—A defeated animal would generally quickly run from the scene of an aggressive encounter (Fig. 22a). On subsequent encounters between the same two animals, the loser, or submissive individual, would often exhibit a rapid retreat at the mere approach of the dominant individual.

Submit.—Both genera exhibited a submissive crouch that was occasionally given by a subordinate animal in response to excessive harrassment by a dominant animal. In both genera, the posture was quite similar; the animal would flatten itself on the ground, belly pressed to the substrate, chin down, ears flattened, eyes partially closed. *Galea* tended to be somewhat more hunched than *Kerodon*. In colony situations (large rooms) a submit can stop

a fight; however, in caged encounters it generally was not effective.

Other aggressive traits described by Rood do not apply here. In addition, I consider the tail-up an aspect of sexual behavior, and I will discuss it in the following section.

Sexual Patterns

Naso-anal.—This was the most common sexual gesture in the two genera. One animal would approach a second, and sniff the anogenital region. In *Galea*, the naso-anal was given by males to females, and frequently was the initiating gesture in a mating chase. *Kerodon* males also sniffed the vaginal area of females, with the frequency of naso-anals being highest as the female approached estrous (Figs. 23, 24). Males would also sniff the anogenital area of juveniles, both male and female, often lifting the rump of the juvenile completely off the ground. Shortly after the colony was established, an adult female was observed giving the

naso-anal gesture to the dominant male on a number of occasions. The female would also nose the fur on the back, neck, and belly of the male. The response of the male to these acts was typically either to ignore the female, or to actively move away.

Chin-rump follow.—This also was a common behavior in both genera (Fig. 24a). A male would approach a female, and place its chin on the female's rump. The female would then attempt to move away, and the male would follow. Each time the male was close enough to the female, he would again attempt to place the chin on the rump. This would often deteriorate into an all-out chase, the female running from the male, and the male following in a hopping, or "stotting" gait, always attempting to place the chin on the rump. In the field, these chases would weave in and out of vegetation and rock crevices. The male would occasionally attempt to bite the rump of the female, apparently to slow or stop her. Often, a male *Kerodon* would place the chin on the neck of the female, also an attempt to impede her flight. *Galea* females generally vocalized (peepy squeaks) while being followed.

Circling.—This was a complex gesture observed only in *Kerodon* (Fig. 25). A male would approach a female either from the front or from the rear. When approaching from the front, the male and female would exchange a nose-nose; from the rear the male would give a naso-anal, then at times place the chin on the back. The male would then begin to circle the female, passing close along her side. He would pass in front of her face, occasionally giving a nose-nose, or pass under the chin of the female. He would then move along the other side to the rear of the female. The male would then repeat the passing, but in the opposite direction. The male would often give another naso-anal and then repeat the process, passing a semicircle around the female, then returning in the opposite direction. The female would remain still, either standing, sitting, or in a submit. When the male returned to the rear of the female, she would often begin to move away, and the male would follow, at times attempting to circle again, and at times initiating a chin-rump follow. The function of circling appeared to be to maintain the female in place, so that the male could mount. Although there was no behavior in *Galea* which resembled circling, the "prowl" as described for *Cavia* by Rood (1972) and the "figure-eight" display in *Dolichotis* (Dubost and Genest, 1974) are both similar.

Foot tapping.—This also was observed only in

Kerodon. A sexually excited male would often rapidly tap the forefeet up and down on the ground. This often occurred during circling, or between mounts. This behavior seems related in structure and function to the rump-tapping described for *Microcavia* (Rood, 1972). A variety of other hystri-comorphs (*Dasyprocta*, *Myoprocta*, and *Dinomys*) show foot-tapping motions (Kleiman, 1974), and a *Microcavia* male will often tap the rump of a female with his forepaws (Rood, 1972).

Copulations.—The basic pattern of copulation, based on the criteria proposed by Dewsbury (1972), was the same for both genera—no lock; intromission of short duration; multiple intromissions; thrusting during intromission; single ejaculation. The number of ejaculations present in *Kerodon*, however, was based on the observation of only a few copulations. As both *Cavia* and *Microcavia* exhibited multiple ejaculations, further observations are necessary to confirm this aspect of the pattern in *Kerodon*. The copulatory position differed between the two genera. *Galea* generally mounted the female in an almost upright position, resting the forepaws on the female's rump. *Kerodon* tended to rest the chest and chin on the female's back and grasped the female behind the shoulders with the forelimbs (Fig. 26). The upright position, however, was also observed in *Kerodon*. The position assumed seems to vary with the degree of sexual excitement of the male, the upright associated with higher levels of excitement. A number of gestures in the female seem to stimulate copulatory behavior in the male. Estrous females would expose the perineum to males. In addition, the simple movement of lowering the head and depressing the body would often stimulate males to mount. Non-reproductive juveniles of both genera would often exhibit mounting behavior, indiscriminantly attempting to mate with adults and juveniles of both sexes. On a single occasion, a juvenile male *Kerodon* achieved intromission on an adult female, but did not exhibit thrusting.

Riding.—This behavior was described by Rood for *Microcavia* and *Cavia*, and was also observed in *Kerodon*. When the female attempted to pull away from the male during mounting, the male would often maintain his grasp, and hang on to the female as she moved away.

Tail-up.—Rood described this act as being a defensive aspect of agonistic behavior; however, here it is considered as sexual in context. In both genera, non-receptive females would respond to male fol-

lows by flattening the back, raising the perineum, and squirting urine backwards onto the male (Fig. 24c). The male would then abruptly halt, shake his head to and fro, and wipe the facial area. Females would often present the tail-up without squirting urine, which was also effective in halting males. An additional gesture employed by females to halt approaching males was the tail-down, which is basically the same as the submissive crouch associated with aggressive behavior (Fig. 24d). Females being followed would suddenly stop and press the body to the ground. This gesture was also surprisingly effective in terminating a mating chase.

VOCALIZATIONS

Galea

Peepy squeaks.—These consisted of a series of bubbly, high-pitched peeps and gurgling noises. This was the most common vocalization. Peepy squeaks seemed to indicate both arousal and/or mild anxiety. Females would often give peepy squeaks while being followed. Subordinate animals would in addition give peepy squeaks while being chased by a dominant animal. Peepy squeaks were also emitted by animals when exploring a strange area, and were highly contagious. They were very common in associations of juveniles, and in fact, any group of *Galea* would occasionally burst into a chorus of peepy squeaks.

Stutter.—The stutter vocalization resembled a nasal snort, and was often given in association with the bark. Both these vocalizations were associated with the aggressor in agonistic encounters, and indicated a high level of aggression.

Squeak.—This was a single, high-pitched note, and, as indicated by Rood, indicates pain. It was commonly given by submissive individuals upon being bitten in an agonistic encounter.

Drumming.—Animals in a high state of anxiety would often drum the elongated feet up and down on the substrate in rapid succession. It was most commonly observed when animals were introduced into a strange enclosure. An adult female was also observed drumming when temporarily separated from her juveniles.

Tooth chatter.—This was another vocalization that appeared to indicate a high level of anxiety. It was observed after aggressive encounters, and was given by the loser.

Bark.—The winner of an aggressive encounter would often bark at the fleeing animal. The domi-

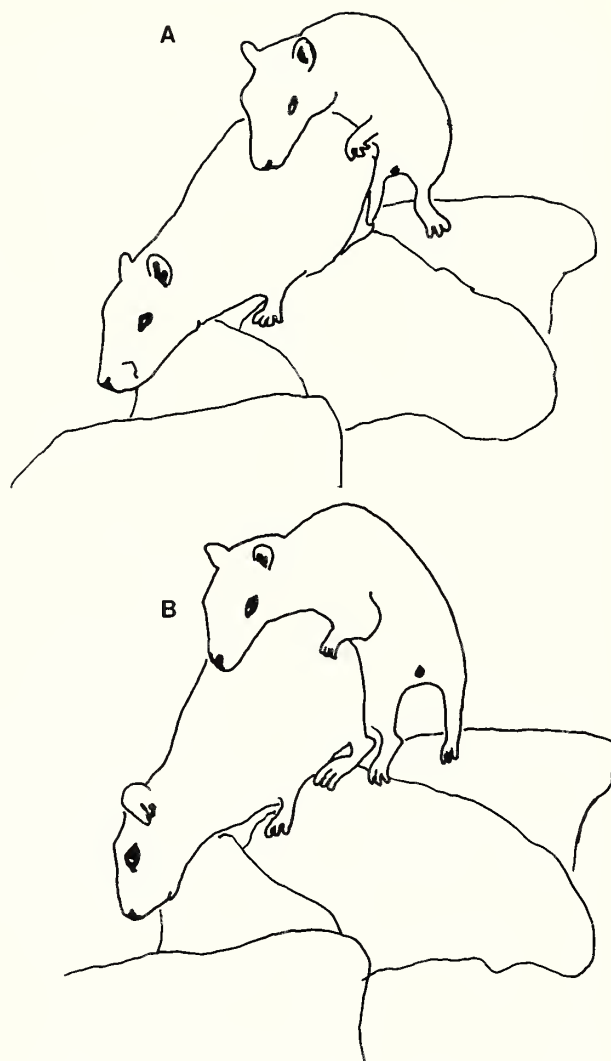


Fig. 26.—Chin on back and attempted mount in *Kerodon* (a and b).

nant animal was by far the most frequent barker, and at times would climb up on top of a pile of rocks (the highest point in the colony) and spend 10 or 15 min barking. Barking, in conjunction with the nasal snort, seemed to indicate both aggression and dominance in *Galea*.

Kerodon

Churr.—This vocalization was very similar to peepy squeaks and was, in essence, a low-pitched version of the same. It was observed in animals which were introduced into the extant colony, and indicated mild anxiety.

Peepy squeaks.—Essentially the same vocalization as in *Galea*, *Kerodon* peepy squeaks tended to

be more restricted in their use. Again, they were common in animals released into strange surroundings, and also were observed in a variety of adult male-female associations, and female-female associations. They were extremely common among juveniles, especially when they were with the adult female. *Kerodon* adults, however, did not give peepy squeaks in aggressive or sexual contexts. Male-female peepy squeaks were given by animals in contact or in close proximity, but were never associated with sexual behavior.

Squeal.—This vocalization was analogous to the *Galea* squeak, but was much louder and much more protracted. Animals would emit a series of high-pitched squeals in response to being captured by hand or being bitten by an aggressor. This vocalization obviously indicated fear and/or pain.

Slow whistle.—An additional vocalization associated with anxiety, the slow whistle consisted of a series of loud whistles, evenly spaced. They tended to be somewhat more muffled than the alarm whistle. They were observed in a number of circumstances. Newborn juveniles would give slow whistles when the female was out foraging. Adults leaving the rocks to forage would also give the slow whistle vocalization. In the field, this almost seemed to function as a communication web, with the animals whistling between one another as they moved out into the trees to forage. More likely, the slow whistle is an anxiety response to leaving the rocks.

Alarm whistle.—Whenever a potential predator moved into rocks occupied by *Kerodon*, the animals began to give an alarm whistle. The vocalization started as a low clucking sound and increased in both pitch and frequency as the source of stimulus approached. The call was given both while the animals were in the open, and when they were down in the rocks. All animals, including *Galea*, would react to the alarm, but the whistle probably reflected high levels of fear and anxiety, as a cornered animal would continue to whistle. Its function as a true alarm call is uncertain (see Discussion).

Nasal hiss.—A rarely observed vocalization of unclear function. The sound resembled a human blowing his nose, and was observed in a number of seemingly dissimilar contexts.

Tooth chatter.—As in *Galea*, an act which indicated nervousness or anxiety. Given by a newly introduced *Kerodon* juvenile while moving about the colony.

SOCIAL ORGANIZATION AND REPRODUCTION

Reproductive Behavior

Galea mating behavior is dominated by the chin-rump follow, whereas *Kerodon* is more characterized by circling. *Galea musteloides* mating behavior is described in detail by Rood (1972) and only the differences observed for *Galea spixii* will be noted here.

All males were observed chin-rump following females, with the frequency being highest as females approached estrous. The churr vocalization was absent in males. Rearing, an extremely common behavior in *G. musteloides*, was also absent in *G. spixii*. *Galea spixii* males exhibit a low tolerance to other males when a female is near estrous, and are extremely aggressive towards males which attempt to follow females. A mating chase, presented in the form of a raw interaction sequence, illustrates quite well the basic format of reproductive behavior in *Galea spixii* (Appendix II).

The chin-rump follow clearly dominates the mating behavior of *Galea spixii*. The practice of placing the chin on the rump has the function of halting the female, so that the male can mount. This was well illustrated during the follow of B13 by MR. When the female does not respond to the male's chin placements, the male often becomes frustrated, and attempts to bite the rump of the female in order to stop her, as was the case when MR followed B3. In general, the female's response largely determines the sequence of events in a *Galea spixii* mating chase (Fig. 27).

Both the gestures involved and the sequencing of these gestures differ in *Kerodon* mating chases. The typical patterns can be observed in the raw interaction sequences (Appendix II). The chase of 3 October 1977 was especially interesting. After the chase, female B was captured, and possessed a copulatory plug. Throughout the chase, the only males to follow were the dominant male, FR; subadult J2, born in the colony; and subadult BR, who was introduced to the colony as a very young juvenile. The number two male, R, introduced as an adult with FR, remained withdrawn throughout the duration of the mating chase.

Although the chin-rump follow forms an integral part of a *Kerodon* mating chase, circling is the most effective behavior in stopping the withdrawal of the female. The placing of the chin most likely serves to inhibit the female tail-up as well as to aid in slowing her retreat. Mating chases are most frequently

Table 5.—Dates of the first observation of selected traits and gestures in *Galea spixii* juveniles. All values in days.

Trait	Individuals							
	BF	FMR	B13	B1	07	08	40	TR
<i>Maintenance and locomotion</i>								
Grooming			22					
Sandbathing			101					
Foraging			11		30		21	3
<i>Aggression</i>								
Chase			101					
Flee	38	38	103	57	35		32	3
<i>Reproduction</i>								
Follow		80	22	60				
Followed			22		60			
Mounting	30							
Thrusting	38							
Tail-up			121					
Vagina open			80					
Testes down	135	135						
<i>Contactual behavior</i>								
Crawl-overs	38	38						
<i>Vocalizations</i>								
Peepy squeaks	15	15						
Bark			119					
<i>Weaning</i>								
	49	49	43	35	42	42		

levels at which the plateaus begin obviously reflect the differences in adult size of the two genera.

Behavioral Development

Kerodon and *Galea* females, like other caviids, give birth to precocial young. Juveniles of both genera were observed moving freely about and foraging at 2 to 3 days of age. Special attention was directed towards juveniles during colony observations, and the first appearance of a variety of traits for both *Kerodon* (Table 4) and *Galea* (Table 5) were noted. Important events concerning changes in reproductive condition were also noted for both genera (Table 6).

Certain aspects of these tables merit closer attention. *Kerodon* exhibit most basic maintenance behavior within a few days after birth. Juveniles run with full coordination, forage on solid food, and exhibit the complete adult grooming repertoire during the first week. The first observed aggressive behavior consists of grappling, which is essentially a type of play-fighting, and fleeing from the aggressive actions of other animals. If the first five aggressive actions against each of the colony-born animals is



Fig. 29.—A one-day old *Kerodon rupestris* female. Note the well-developed hindlimbs.

examined, it is found that 76.6% of the aggressors were either adult females other than the mother, or other colony-born juveniles. These results will be treated in more detail in the section on aggressive behavior.

Kerodon juveniles do not exhibit more active aggressive behavior until a much later date. Chasing is observed first, well before lunging behavior. Lunges tend to be given by animals of high dominance, or by aggressors who hold a decided advantage over their opponent, thus would be expected to appear later than simple chases. Play-fighting, or grappling, is last observed shortly after the appearance of lunging behavior. The submissive posture also first appears at approximately this time.

Table 6.—A comparison of the time of onset of selected reproductive characteristics in *Kerodon* and *Galea*. Times with a sample size of $N \geq 2$ are presented \pm one standard deviation.

Reproductive characteristic	<i>Kerodon</i>	<i>Galea</i>
Weaning	35.17 \pm 10.1 days N = 6	42.25 \pm 5.7 days N = 4
Males testes descended	115 \pm 2.7 days N = 4	135 \pm 0 days N = 2
Female vagina open (earliest observation)	60 days	80 days
Earliest pregnancy observed	81 days	102 days
First partum	156 days	no data

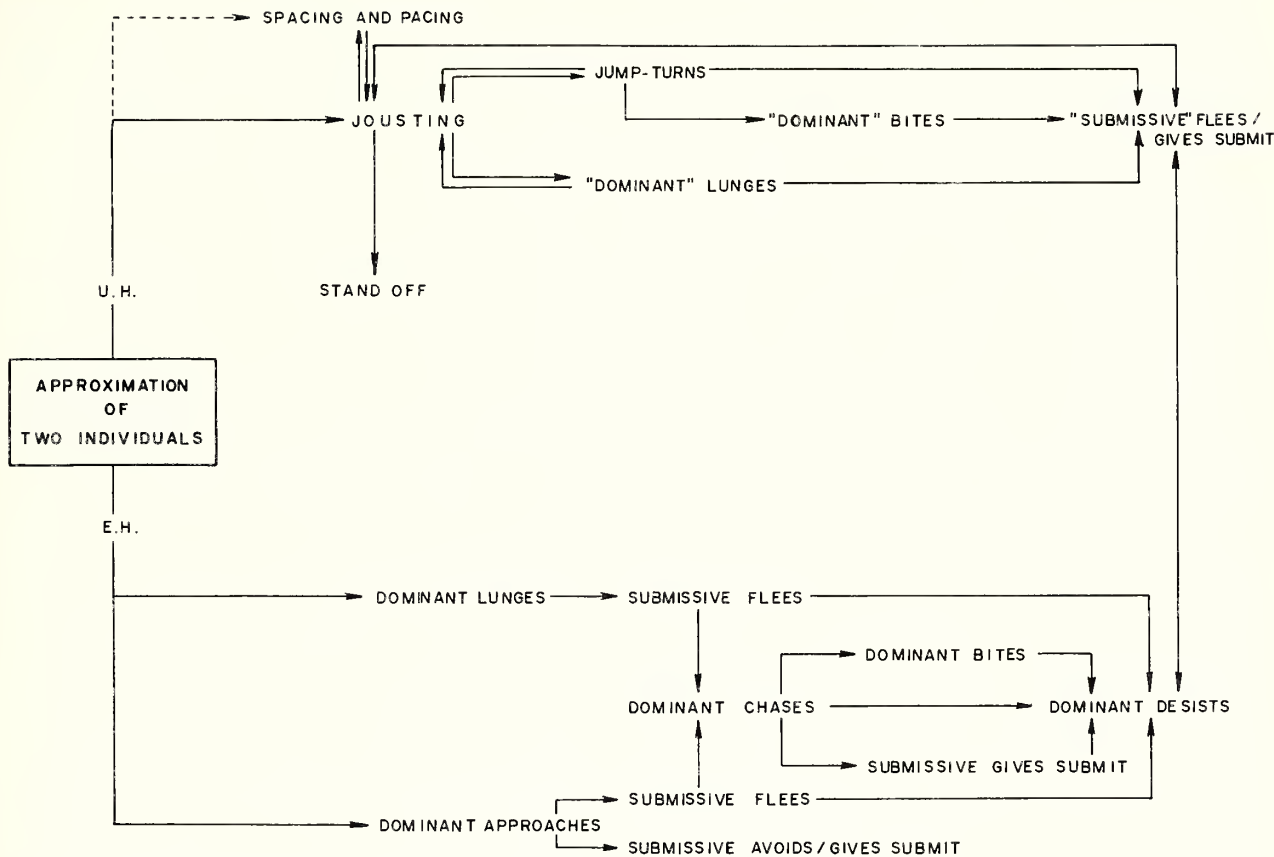


Fig. 31.—Sequence of aggressive gestures in *Kerodon*. *Kerodon*, as with *Galea*, presents two different sequences of aggressive behavior—one for unestablished hierarchies (U.H.) and one for established hierarchies (E.H.). The major difference from the *Galea* sequence is the substitution of the curved-body posture by jousting, and occasionally spacing and pacing.

The sequence of gestures in a given *Galea* aggressive encounter therefore will differ, depending upon the density of the population or the degree of familiarity of the animals (Fig. 30). After the establishment of the hierarchy in the permanent *Galea* colony, curved body postures were observed only twice in 307 aggressive encounters (.65%), and thus are not included as part of the normal behavioral sequence for established hierarchies. The submit posture was rarely observed in the colony, and occurred primarily in situations of unestablished hierarchies. Curved-body postures occasionally terminated in a stand-off, with both animals withdrawing simultaneously.

As with *Galea*, *Kerodon* aggressive behavior varies with the degree of familiarity and rigidity of the relationship between the animals (Fig. 31). The sequence of aggressive acts for established hierarchies is the same for both *Kerodon* and *Galea*. There are a few minor differences in the sequence

of events for non-established hierarchies. The curved-body posture is conspicuously absent from *Kerodon* aggressive behavior. The uncommon gesture spacing and pacing, in combination with jousting, seems to occupy the functional position of the curved-body posture.

This similarity in gestures and sequences is especially obvious in interspecific encounters. When an individual *Galea* presents the curved-body posture to a *Kerodon*, the latter will align its body in parallel to the former; *Kerodon*, however, does not curve its body. In response to a *Galea* lunge, a *Kerodon* exhibits jump-turns exactly as if it were a *Kerodon-Kerodon* encounter. *Kerodon* tend to simply avoid aggressive moves by *Galea* by jump-turning away; however, if provoked, they easily dominate *Galea* because of their larger size, superior agility, and jumping ability.

Interestingly, the flow of aggressive gestures for well-established hierarchies is unidirectional, as the

Table 7.—Summary of aggressive behavior observed in the Galea colony between September 1977 and March 1978. A = approach; L = lunge; C = chase. Losses mean the animal either fled or gave a submissive display in response to the aggressor's action.

Animals	Wins			Losses		
	A	L	C	A	L	C
<i>Males</i>						
MR	5	19	13	0	0	0
BM	0	10	46	2	4	27
FR	0	1	6	0	5	26
FMR	0	1	4	1	9	57
BF	0	1	2	4	3	45
B2R	0	0	0	0	0	6
B2M	0	0	0	0	1	1
Total	5	32	171	7	22	162
<i>Females</i>						
F	5	9	22	0	4	3
B3	5	2	15	2	8	10
R	0	5	25	2	0	17
M	0	0	3	3	5	26
B2	0	0	4	1	5	7
B13	0	0	4	0	0	11
B1	0	0	0	0	2	4
B1J	0	0	0	0	1	2
40	0	0	0	0	1	2
Total	10	16	73	8	26	82

outcome is predictable before the encounter. There is a built-in cycle in the flow of aggressive behavior for non-established hierarchies. This cycle will often be repeated five or six times in a single aggressive encounter. When the relationship between the two animals is not established, exactly which animal takes the initiative (that is, the "dominant" individual) will often change each trip through the cycle until one animal emerges as the convincing victor. Being the winner of a single bout, however, is often not sufficient to definitively set the hierarchical relationship. The "submissive" individual (after a loss) will often initiate another bout with the victor by assuming a curved-body posture or by jousting. The order is often reversed in this manner, the final established hierarchy being determined through the action of numerous encounters between the newly introduced members of the colony.

Galea females were overtly aggressive towards one another beginning on the day of introduction into the colony. *Kerodon* females, on the other hand, exhibited amicable, or neutral, relations towards one another throughout the first few months. All initial aggression was male-male. If each female

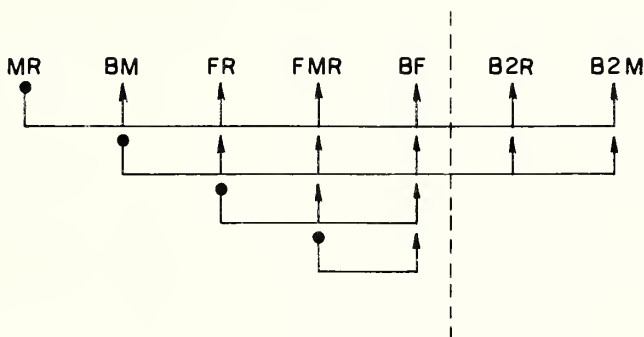
Table 8.—Summary of aggressive behavior observed in the Kerodon colony between September 1977 and March 1978. See Table 7 for explanation. A = approach; L = lunge; C = chase.

Animals	Wins			Losses		
	A	L	C	A	L	C
<i>Males</i>						
FR	23	26	52	0	0	0
R	3	6	3	17	22	49
BR	3	2	16	2	17	19
J2	1	1	6	4	7	21
J5	0	2	3	1	3	2
B2	0	0	0	0	1	0
B3	0	0	0	0	1	2
Total	30	37	80	24	51	93
<i>Females</i>						
B	1	9	31	0	0	1
F	0	8	5	1	2	10
J	0	5	23	1	4	10
JR	0	3	4	2	3	21
B1	0	0	0	0	1	6
JF	0	0	0	3	1	0
M	0	0	0	0	0	2
Total	1	25	63	7	11	50

is examined separately, an interesting pattern emerges. The onset of aggressive behavior for each colony female coincides with the first pregnancy for that female. Thus the complete five-female hierarchy was not established until the first pregnancy of JR. Although difficult to demonstrate quantitatively, adult females were qualitatively far more aggressive while pregnant. In addition, of six juveniles born after 17 December (that is, the date on which all four adult females were pregnant), four died within a week to 10 days after birth. At least one of these deaths was due to a failure of lactation in the female. This high level of juvenile mortality is probably related both to female-female aggression, causing, for example, failure of lactation due to stress, and to adult female-juvenile aggression, which is especially common between females other than the mother, and young juveniles. This high level of female aggression is probably common in the field, as the initial time period after the establishment of a colony represented a rather unnatural situation. Field observations on *Kerodon* indicated an absence of periodicity of reproduction, and a reasonable proportion of the population is probably pregnant at any given time.

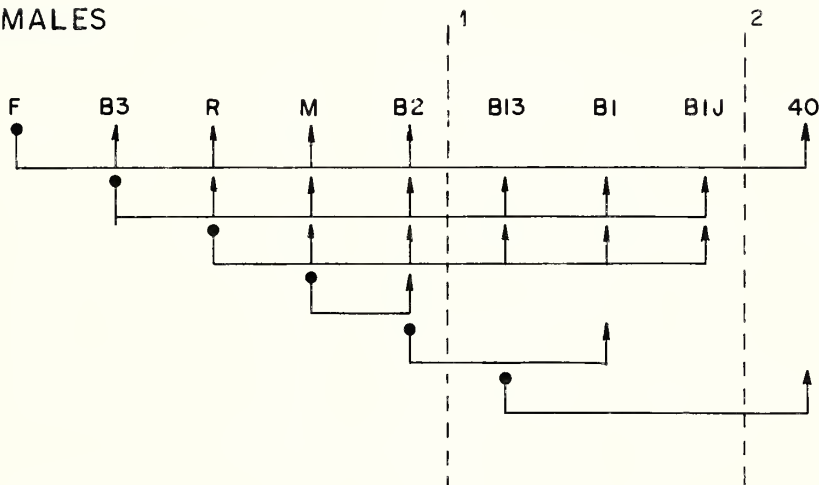
Although the sequence of gestures in an aggressive encounter is almost identical for *Kerodon* and *Galea*, if the overall patterns of aggression within

a) MALES



$h = 1.00$

b) FEMALES



$h_1 = 1.00$

$h_2 = .548$

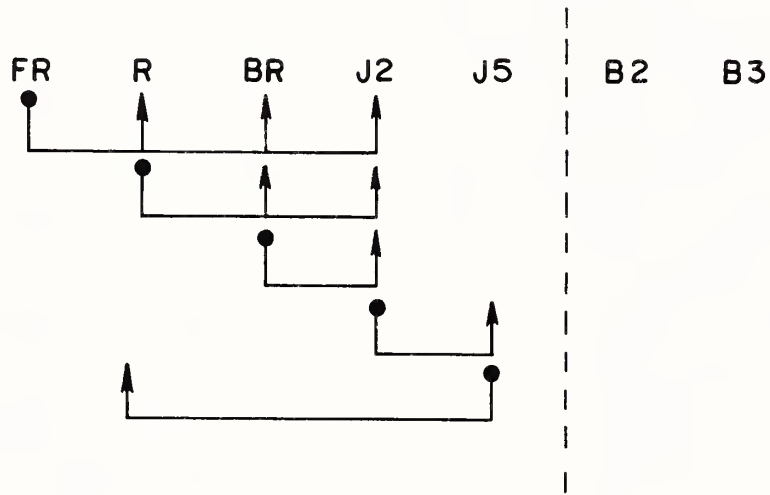
Fig. 32.—*Galea* male (a) and female (b) hierarchies. The dominant animal in a given sequence is indicated by a dot and the animals it dominates by arrows. Only animals located left of the dotted lines were used in calculating h . The calculation h for females includes only sexually mature adults. The value h_2 includes adults and juveniles. The male h value is for sexually mature adults.

each colony are examined, some notable differences emerge. All aggressive encounters recorded in both the *Galea* and *Kerodon* colonies between September 1977 and March 1978 were tabulated (Tables 7–8). As hierarchies were already well established at this time, aggressive actions for dominant individuals could be expressed as either approaches in an aggressive posture, lunges, or chases. The submissive response was classified as

a “flee” from one of the above three dominant actions. In addition to the summary tables presented, an individual record for each animal was compiled in order to examine hierarchical relations, differences in use of aggressive gestures and intersexual aggression.

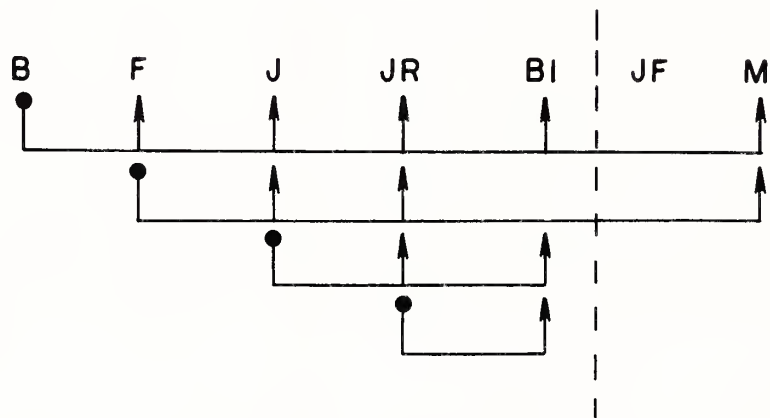
Rank in the hierarchies was determined through the balance of aggressive encounters between all possible pairs of individuals of the same sex. The

a) MALES



h = .400

b) FEMALES



h = .900

Fig. 33.—*Kerodon* male (a) and female (b) hierarchies. The organization is the same as Fig. 32. Animals left of the dotted line are introduced adults or juveniles which became reproductive adults during the course of the study.

rankings obtained were used to calculate an index of linearity (h), using Landau's method (Bekoff, 1977). The index of linearity varies between 0 and 1, and is calculated by the formula

$$h = \frac{12}{n^3 - n} \sum_{a=2}^n \left(V_a - \frac{n-1}{2} \right)^2,$$

where n = the number of individuals in the hier-

Table 9.—Summary of the comparisons of various aspects of aggressive behavior for the *Kerodon* and *Galea* colonies. Although no direct comparisons are made between the two colonies, there are some marked differences present in the organization of agonistic behavior.

Characteristic	<i>Kerodon</i>	<i>Galea</i>
Comparison of mean aggressive encounters between sexes (excluding juveniles)	Males: mean = 61.4 Females: mean = 32.75 ($t_s^1 = 1.62$, $df = 4, 3$; ns)	Males: mean = 76.4 Females: mean = 32.0 ($t = 2.79$, $df = 9$; $P < 0.05$)
Comparison of variation in aggressive encounters between males and females (excluding juveniles)	Males: $S^2 = 1,489.3$ Females: $S^2 = 54.25$ $F_{max} = 27.45$, $df = 3$; $P < 0.05$	Males: $S^2 = 1,286.3$ Females: $S^2 = 207.4$ $F_{max} = 6.20$, $df = 4$, ns
Linearity of hierarchy	Males: $h = 0.400$ Females: $h = 0.900$	Males: $h = 1.000$ Females: $h = 1.000$
Both sexes use approaches plus lunges and chases in the same proportions.	$\chi^2_{adj} = 5.55$; $P < 0.025$	$\chi^2_{adj} = 2.457$; $P > 0.10$
Intrasexual aggression occurs with the same frequency for both sexes.	$\chi^2_{adj} = 28.47$; $P < 0.005$	$\chi^2_{adj} = 0.90$; $P > 0.10$

archy and V_a = the number of individuals dominated by animal *a*. Hierarchies with a rating of 0.9 or higher are considered strongly linear.

Galea hierarchies (Fig. 32) are linear for both males and females. *Kerodon* females also possess linear hierarchies; however, males show a very weakly linear relation (Fig. 33). The *Kerodon* male hierarchy is even weaker when the two juveniles excluded from the calculations are considered. Both B2 and B3 were present in the colony for the same amount of time as was juvenile female B1. Female B1 was aggressively attacked by three different adult females in the colony. Only her mother, F, was nonaggressive. Males B2 and B3, on the other hand, were involved in a total of only four aggressive encounters, all with females. They were involved in no aggressive encounters with males, thus by definition could not be included in the calculations of hierarchy linearity. The hierarchy, in reality, should be considered even less linear than is indicated by the *h* value.

Aggression between adults and juveniles is at its minimum among *Kerodon* males (Fig. 33). The dominant male, FR, directed only 12 of 101 aggressive actions against juveniles. Eight of the 12 were against BR, a male introduced into the colony as a juvenile. Only four aggressive gestures were directed against the 12 juveniles actually born in the colony. *Kerodon* females are aggressive towards juveniles other than their own progeny. Female F, in addition, was aggressive towards her daughter, JR, when JR was in late pregnancy.

There is no obvious pattern in *Galea* adult-juvenile aggression. Adults are aggressive towards

other juveniles, as well as their own progeny (Fig. 32).

Galea males were involved in 382 aggressive encounters during the observations, with a mean of 76.4 ± 35.9 SD per animal. *Galea* females, for the same number of hours of observation, were involved in 192 encounters with a mean of 32.0 ± 14.4 SD encounters per female. These mean values are significantly different ($t = 2.79$, $df = 9$, $P < 0.05$). The variance of aggressive encounters among males ($S^2 = 1,286.3$) was much larger than among females ($S^2 = 207.4$); however, the difference is not significant. The above calculations include only encounters involving adults. All encounters involving juveniles were eliminated, as the potential number of encounters varies with the amount of time that each juvenile was present.

The *Kerodon* data were analyzed in the same manner. Males were involved in 307 encounters, giving a mean of 61.4 ± 38.6 SD encounters per individual. As with *Galea*, the females were involved in fewer encounters, 131, with a mean of 32.75 ± 7.4 SD per animal. The variances of aggressive encounters for males ($S^2 = 1,489.3$) and females ($S^2 = 54.25$) were significantly different ($F_{max} = 27.45$, $df = 3$, $P < .05$). Means were thus compared using a *t*-test for unequal variances. There was no significant difference ($t_s^1 = 1.62$, $df = 3$, $P > 0.1$).

All agonistic actions were recorded as either "approaches," "lunges," or "chases." The frequency of use of each of these various gestures was compared between males and females of both genera. The data used were the same as in the previous

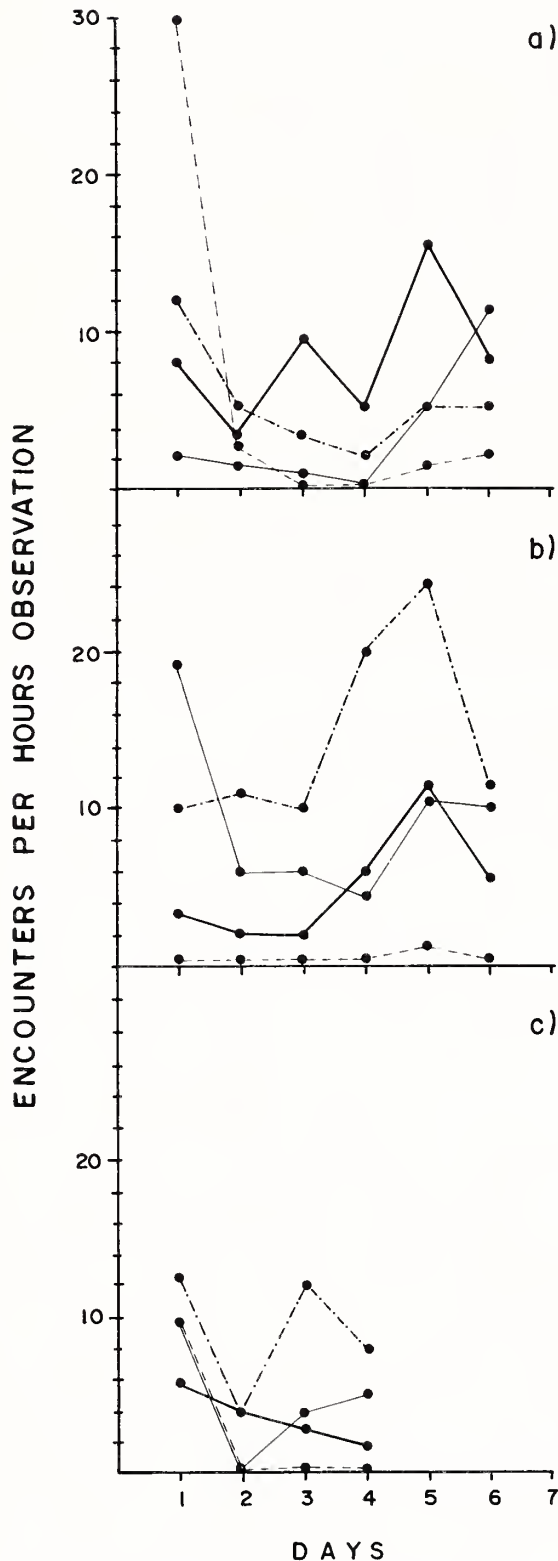


Fig. 34.—Relationships between the number of encounters observed per hour and the number of days that the colony was in existence for (a) a simultaneous introduction of both species

analysis. The number of “approaches” was extremely small for both *Galea* and *Kerodon*. Given the functional similarities between “approaches” and “lunges” (high superiority), the two gestures were combined for the analysis. *Galea* males used high and low superiority gestures in the same proportions as females ($\chi^2_{\text{adj}} = 2.457, P > 0.10$), while *Kerodon* males utilized a higher proportion of “superior dominance” gestures than females ($\chi^2_{\text{adj}} = 5.55, P < 0.025$).

Finally, inter- and intrasexual aggression were compared for the two genera. Data for both adults and juveniles were used for these analyses. The hypothesis that neither sex interacts disproportionately with the other was tested for *Galea* and *Kerodon*. The hypothesis was accepted for *Galea* ($\chi^2_{\text{adj}} = 0.9, P > 0.10$) and rejected for *Kerodon* ($\chi^2_{\text{adj}} = 28.47, P < 0.005$). *Kerodon* males interact primarily with males, whereas females interact equally with both sexes. These data are related to the male FR-R conflict. There was no aggression between FR and his harem females, and little aggression towards females by the juveniles. The actual number of aggressive encounters between FR and R was large. These encounters generally involved FR keeping R away from the rocks or the females, a process involving an already established hierarchy. High superiority gestures dominated in these situations. There was aggression between R and the progeny of FR, but levels were low because of the vigilance of FR in guarding the rocks. There is a straight-line hierarchy within juveniles (Fig. 33), a factor which may be important in juvenile emigration, but again, levels are low. The result is the non-linear hierarchy and the high variance. The various comparisons of patterns of aggression within each genus are summarized in Table 9.

Once the colonies were established, it was nearly impossible to introduce an additional animal. An adult female introduced into the *Kerodon* colony was killed in two days, and a subadult male was antagonized to such a degree that it was necessary to remove him after a few hours. Only juvenile BR was successfully introduced, and the colony con-

←
into an arena; (b) *Galea* introduced into a *Kerodon* colony; and (c) *Kerodon* introduced into a *Galea* colony. Both intraspecific and interspecific encounters are represented. The thin solid line represents *Kerodon* wins over *Galea*, and the dotted line illustrates *Galea* wins over *Kerodon*. Intraspecific aggression is represented by the heavy solid line (*Galea*) and the dot and dash line (*Kerodon*).

tained only seven animals at the time. Any animals introduced into the *Galea* colony were subjected to such violent aggressive actions by the dominant animals that they would probably have been killed had they not been removed. A large adult male introduced one evening was scarred and bloody the following morning and had lost 10% of its body weight.

In order to evaluate the level of interspecific aggression between the two genera, data were collected on three mixed colonies—one in which both genera were introduced simultaneously; a second in which *Kerodon* were added to an existing *Galea* colony; a third in which *Galea* were added to a *Kerodon* colony. An hourly encounter rate for both intraspecific and interspecific aggression was calculated, and the daily trends in aggression compared for all three colony situations (Fig. 34). The mean encounters per hour for intraspecific aggression fluctuate from day to day for both genera. The trend in interspecific aggression varies with the colony condition. When both genera were released simultaneously, the smaller *Galea* initially dominated the larger *Kerodon*. After 2 days the trend reversed, however, and *Kerodon* assumed an aggressive superiority. When *Kerodon* were introduced into a *Galea* colony, interspecific aggressive actions were equal for the first 2 days, after which *Kerodon* again assumed a superiority. *Galea* were completely dominated when placed in a established *Kerodon* colony. Apparently, *Kerodon* can aggressively exclude *Galea*. In the case in which *Galea* were introduced, the 15 animals of the *Galea* colony used throughout the study were placed in the large *Kerodon* room with the 14 resident animals. *Kerodon* were extremely aggressive towards *Galea* in and near the rocks, and by 6 days had effectively forced the *Galea* to utilize the field, brush pile, and forest areas. When startled, *Galea* fled into the rocks, but after a delay of 1 to 5 min *Kerodon* would no longer tolerate the *Galea* and would aggressively force them out.

Galea probably use rock piles in the wild for temporary escape from predators. The aggressive pressure of *Kerodon* on *Galea* is probably less in the wild than in the mixed colony, as the natural habitat is structurally more diverse, offering potential refugia to *Galea*. Microhabitat analyses, however, indicated that *Galea* were significantly more abundant in the forest thickets than in the other microhabitats, and these data, coupled with the above observations, strongly imply that *Galea* is actively excluded from the rocks by *Kerodon* aggression.

Interspecific aggression was also examined by colony condition and type of gesture. The relative proportions of *Kerodon* and *Galea* wins were tested for all three colony conditions. *Kerodon* won a significant proportion of interspecific encounters only when *Galea* were introduced into the *Kerodon* colony ($\chi^2 = 78.19$, $df = 1$, $P < .005$). *Kerodon* superiority in the other two colonies was counterbalanced by the high level of *Galea* dominance during the first 2 days.

The use of "approaches," "lunges," and "chases" was compared between encounters in which *Kerodon* won and in which *Galea* won. There was no significant difference when all three colony situations were summed ($\chi^2 = 0.428$, $df = 2$, $P > 0.05$). When each colony condition was examined separately for both *Kerodon* wins and *Galea* wins, *Kerodon* utilized a significantly greater proportion of "chases" when attacking *Galea* introduced into the *Kerodon* colony ($\chi^2 = 45.21$, $df = 2$, $P < .005$). Similarly, *Galea* used a significantly greater proportion of "chases" when attacking *Kerodon* introduced into the *Galea* colony ($\chi^2 = 1.86$, $df = 2$, $P < 0.005$). In all other situations, the proportions of the three gestures did not differ. These data support the assumption made earlier that there exists a functional difference between the three gestures. "Approaches" and "lunges" reflect a high degree of superiority of the aggressor. "Chases" are used in situations in which superiority has not yet been established, as when strange animals are introduced into an established colony.

The "*Galea* introduced" mixed colony was examined in more detail than the other two, as two established colonies were combined. The animals used were those that had been maintained together for the duration of the major part of this study. It was thus possible to observe interspecific aggression between two populations with known established hierarchies.

Aggression by *Kerodon* against *Galea* was examined for each animal in relation to its position in the hierarchies. *Kerodon* males and females were equally aggressive towards *Galea* ($\chi^2 = .59$, $df = 1$, $P > 0.05$); however, *Galea* males were attacked more frequently than females ($\chi^2 = 13.76$, $df = 1$, $P < 0.005$). If *Kerodon* interspecific aggression is examined case by case, both females and males were disproportionately aggressive towards *Galea* males ($\chi^2 = 27.72$, $df = 1$, $P \ll 0.005$). It was previously shown that *Galea* males are involved in significantly more intraspecific encounters than fe-

Table 10.—Observed and expected capture frequencies for the five major species on the grid. The underlined pair of numbers for each species indicate the point of greatest divergence from the theoretical distribution. The differences, *D*, were tested at $P = .05$ (Siegal, 1956). C.F.D. = Cumulative frequency distribution of traps per microhabitat type, beginning with the rarest and successively adding each more common microhabitat.

Microhabitat	C.F.D.	<i>Galea</i>		<i>Kerodon</i>		<i>Trichomys</i>		<i>Monodelphis</i>		<i>Didelphis</i>		Total	
		Observed	Expected	Observed	Expected	Observed	Expected	Observed	Expected	Observed	Expected	Observed	Expected
<i>Cnidoscopus</i>													
flat	.007	3	1.61	0	.04	0	.20	0	.28	0	.32	3	2.45
Cultivated area	.027	7	6.21	0	.16	2	.76	1	1.08	3	1.24	13	9.45
Scrub flat	.054	14	12.42	0	.32	2	1.52	1	2.16	4	2.48	21	18.90
Grassy area	.107	27	24.61	0	.64	5	3.00	2	4.28	6	4.92	40	37.45
Thorn thicket	.414	117	95.22	0	2.48	9	11.60	16	16.56	21	19.04	163	144.90
Boulder area	1.000	230	230	6	6.00	28	28.00	40	40.00	46	46.00	350	350.00

males. This higher level of aggressiveness in males may have provoked the response of *Kerodon* males and females. There are few gestural differences in the repertoires of aggressive behavior between the two genera, and the sequences are also quite similar.

Within *Kerodon* males, the frequency of aggressive acts was not equally distributed among all individuals, even when young juvenile J13 was eliminated ($\chi^2 = 63.69$, $df = 6$, $P < 0.005$). The number two male, R, exhibited 57.9% of the aggressive activity against *Galea*. Male R was the only nonresident of the "harem" of dominant male FR. *Kerodon* females, with juvenile J14 eliminated, were also aggressive in unequal frequencies ($\chi^2 = 53.78$, $df = 4$, $P < 0.005$). The number four and five females in the hierarchy, JR and B1, exhibited 91.1% of the aggression. On the other hand, *Galea* males (B2M eliminated) were all attacked in equal proportions ($\chi^2 = 4.93$, $df = 4$, $P > 0.10$). The small sample size for *Galea* females prohibits a statistical analysis, but aggression is approximately evenly distributed throughout the hierarchy.

Use of Space

Only *Galea* were live-trapped in sufficient numbers to be able to calculate home range sizes. Male home ranges averaged 872 ± 497 SD m^2 and females averaged 632 ± 978 SD m^2 ; however, there was no significant difference between sexes (t -test adjusted for unequal variances; $t_s^1 = 619$, $P > .5$).

Live-trap data were also used to calculate microhabitat preferences, not only for *Kerodon* and *Galea*, but for other mammals present on the grid as well. The objective of the microhabitat analysis was

to determine if the two genera differed in their microhabitat distributions. The other species, none of which was a likely competitor with the caviids, were included in the analysis to provide material for comparison.

A cumulative frequency distribution of traps by microhabitat type was constructed based upon the habitat analysis results. Deviations from this expected cumulative frequency distribution of captures were tested by the Kolmogorov-Smirnov one-sample test (Table 10). Only *Galea* showed a deviation from the theoretical distribution, being significantly overabundant in the *Croton* thickets, the microhabitat type which is physically adjacent to the rockpiles. *Kerodon* was captured only in the rocks, and although the sample size was too small to indicate a significant preference for this habitat, visual observations of 25 marked individuals indicated that this species is a habitat specialist. All other species are randomly distributed throughout the six microhabitats. These data indicate either a *Galea* preference for *Croton* thickets or an exclusion of *Galea* from the rocks, leading to an overabundance in the habitat bordering the rockpiles. *Galea* were constantly observed fleeing or retreating into the rocks at my approach, and showed no obvious aversion to the rock areas. Also, *Croton* thickets have little low vegetation available for forage by *Galea* to support the observed population densities. The thickets offer little protection from predators. These observations, coupled with the data on aggression in mixed colonies, suggest that *Galea* utilize the rocks as temporary refugia from danger but are continually forced out by aggression from *Kerodon*.

Table 11.—Summary of the five time budget tables in relation to four broad categories of behavior. All five groups spend the majority of their time in various aspects of maintenance behavior. All values except the activity ratio are percentages. The activity ratio is equal to time inactive plus time sitting divided by total time.

Behavior	Kerodon			Galea	
	Males	Females	Juveniles	Males	Females
Maintenance	98.34	98.77	99.01	99.17	99.73
Aggression	0.26	0.15	0.33	0.48	0.21
Reproduction	0.73	0.45	0.34	0.06	0.06
Contact	0.06	0.50	0.32	0.29	0.00
Activity-ratio	0.089	0.108	0.145	0.595	0.584

Time Budgets and Analysis

Time budgets were compiled for *Kerodon* adult males, adult females, and juveniles (sexes combined) as well as *Galea* adult males and females (Lacher, 1980). Each time budget presents the average percent time an individual of a given group was observed to perform a given behavioral act. An activity ratio (time active divided by total time) is also presented for all five groups.

Both genera spend the great majority of their time involved in various aspects of maintenance behavior (Tables 1, 11). The sum of aggressive, reproductive, and contact-promoting behaviors represents approximately 1% of the time budget for each group. Activity ratios were quite different between *Kerodon* and *Galea*, with *Galea* active a much greater proportion of the time. This difference was associated with the large amount of time that *Galea* spends foraging as compared to *Kerodon*.

In comparisons of the percent time spent in a given activity, some variables (for example, grooming) were quite consistent among groups. Other variables indicate basic divergences between groups in the allocation of time. *Kerodon* males, females, and juveniles spent 1.29, 0.09, and 3.81%, respectively, of their time foraging, whereas *Galea* males spent 55.07% and females 52.12%. These data were collected for all groups approximately 12 h after food was presented. Both genera are herbivorous, *Kerodon* feeding primarily on leaves and *Galea* on grass. There were no major differences in caloric or ash content in the plant species presented to the colony animals (G. Eiten, personal communication) and there is no likely physiological reason for the difference in time allocation. One possible explanation is that individual leaves of grass, particularly younger shoots, are much lighter than, for example, an individual tree leaf of *Ziziphus joazeiro* or *Cro-*

ton jacobinensis. *Galea* spend more time foraging simply because it takes more time to collect a sufficient mass of food.

Kerodon females and juveniles spend much more time "inactive" (for example, down in the rocks), than the other three test groups. Although females frequently emerge to nurse young, they undoubtedly nurse while in the rocks as well. Also, females spend more time in the rocks even without young, as the function of territorial defense is assumed by the dominant male.

Mean population-durations, standard deviations, and coefficients of variation were calculated for all five groups for which time-budget data were collected (Table 12). Within group variances for a number of behavioral acts were obviously quite different from group to group. In order to attempt to determine which acts were important in separating the groups, a Kruskal-Wallis one-way analysis of variance by ranks was performed to compare the five populations (Siegel, 1956). Fourteen variables were statistically different among the groups (Table 13). A distribution-free multiple comparisons test based on Kruskal-Wallis rank sums (Hollander and Wolfe, 1973) was used to compare the average ranks of the above variables for the five groups tested. This comparison allows for unequal sample sizes, and is a more conservative procedure than the test used for equal sample sizes. The experiment-wise error rate was set at 0.05. Four variables are effective in separating *Galea* adults from the *Kerodon* groups: sitting rocks, sitting-ground, foraging, and activity ratio (Fig. 35). *Kerodon* juveniles cannot be separated from adults females, but are statistically different from adult males in relation to two variables—inactive (that is, in the rocks) and sitting in the trees. Based on Kruskal-Wallis rank sums, no variables were effective in separating adult males and females from one another for either *Kerodon* or *Galea*.

Sexes were compared within each genus by a Mann-Whitney U-test for two samples. Seven variables were effective in separating male and female populations in *Kerodon* (inactive, sitting-trees, nursing, lunging, following, followed, crawl-overs), whereas only one variable, foraging, differed between male and female *Galea*.

Although a variable by variable analysis is useful in indicating which traits differed between groups, such analyses do not permit a classification of individual samples in populations. In addition, a variable by variable analysis will be less effective in

					→
INACTIVE	<u>KM</u>	<u>GF</u>	<u>GM</u>	<u>KF</u>	<u>KJ</u>
SIT-ROCKS	<u>GF</u>	<u>GM</u>	<u>KJ</u>	<u>KM</u>	<u>KF</u>
SIT-GROUND	<u>KJ</u>	<u>KF</u>	<u>KM</u>	<u>GF</u>	<u>GM</u>
SIT-TREES	<u>GM</u>	<u>GF</u>	<u>KJ</u>	<u>KF</u>	<u>KM</u>
SIT-SAND	<u>KM</u>	<u>KF</u>	<u>KJ</u>	<u>GF</u>	<u>GM</u>
CLIMBING	<u>GM</u>	<u>GF</u>	<u>KJ</u>	<u>KF</u>	<u>KM</u>
WALKING	<u>KF</u>	<u>KJ</u>	<u>KM</u>	<u>GF</u>	<u>GM</u>
SUCKLE	<u>GM</u>	<u>GF</u>	<u>KM</u>	<u>KF</u>	<u>KJ</u>
NURSING	<u>KJ</u>	<u>KM</u>	<u>KJ</u>	<u>GM</u>	<u>GF</u>
FORAGING	<u>KF</u>	<u>KM</u>	<u>KJ</u>	<u>GM</u>	<u>GF</u>
GRAPPLING	<u>GM</u>	<u>GF</u>	<u>KF</u>	<u>KM</u>	<u>KJ</u>
FOLLOWING	<u>KJ</u>	<u>KF</u>	<u>GF</u>	<u>GM</u>	<u>KM</u>
CRAWL-OVER	<u>GF</u>	<u>KM</u>	<u>GM</u>	<u>KF</u>	<u>KJ</u>
ACTIVITY-RATIO	<u>KF</u>	<u>KM</u>	<u>KJ</u>	<u>GM</u>	<u>GF</u>

Fig. 35.—Results of the distribution free multiple comparisons test based on Kruskal-Wallis rank sums (Hollander and Wolfe, 1973) for 14 significant variables. Groups are listed in order from lowest mean rank (left) to highest mean rank (right). All non-significantly different groups are connected by the same line. GM = *Galea* males; GF = *Galea* females; KM = *Kerodon* males; KF = *Kerodon* females; KJ = *Kerodon* juveniles. Experiment-wise error rate = 0.05.

Table 12.—Mean population-durations \pm one standard deviation for 28 variables for two Galea groups and three Kerodon groups. Coefficients of variation are given in parentheses.

Variable	Group					Total
	Galea males	Galea females	Kerodon males	Kerodon females	Kerodon juveniles	
Inactive	32.79 \pm 27.7 (0.8)	34.01 \pm 53.2 (1.6)	8.94 \pm 15.7 (1.8)	174.93 \pm 484.6 (2.8)	132.25 \pm 212.6 (1.6)	76.34 \pm 235.8 (3.1)
Sit rocks	10.04 \pm 29.4 (2.9)	0.00	35.28 \pm 42.8 (1.2)	42.64 \pm 36.1 (0.8)	31.05 \pm 22.4 (0.7)	25.30 \pm 33.7 (1.3)
Sit ground	30.41 \pm 22.4 (0.7)	48.41 \pm 58.5 (1.2)	14.82 \pm 30.8 (2.1)	9.74 \pm 15.5 (1.6)	4.87 \pm 5.6 (1.2)	20.03 \pm 33.7 (1.7)
Sit trees	0.00	0.00	125.69 \pm 144.0 (1.1)	186.35 \pm 496.0 (2.7)	6.54 \pm 10.7 (1.6)	66.07 \pm 231.1 (3.5)
Sit sand	7.38 \pm 12.6 (1.7)	1.22 \pm 2.9 (2.3)	0.00	0.00	0.00	1.47 \pm 5.8 (4.0)
Running	1.59 \pm 0.7 (0.5)	2.05 \pm 0.9 (0.4)	2.06 \pm 1.1 (0.5)	2.06 \pm 0.9 (0.4)	2.09 \pm 1.6 (0.8)	1.98 \pm 1.1 (0.6)
Climbing	0.00	0.00	1.80 \pm 1.5 (0.9)	1.45 \pm 2.3 (1.6)	0.59 \pm 1.0 (1.8)	0.84 \pm 1.5 (1.8)
Walking	2.96 \pm 1.9 (0.7)	1.94 \pm 1.6 (0.8)	1.48 \pm 2.3 (1.6)	0.57 \pm 1.1 (2.0)	1.11 \pm 1.4 (1.3)	1.56 \pm 1.9 (1.2)
Sandbathing	0.33 \pm 1.2 (3.5)	0.33 \pm 1.2 (3.5)	0.00	0.00	0.00	0.11 \pm 0.7 (5.9)
Grooming	4.51 \pm 3.2 (0.7)	4.56 \pm 1.8 (0.4)	5.81 \pm 4.0 (0.7)	3.48 \pm 2.5 (0.7)	4.75 \pm 3.6 (0.8)	4.70 \pm 3.2 (0.7)
Suckling	0.00	0.00	0.00	0.00	38.11 \pm 64.9 (1.7)	8.71 \pm 34.3 (3.9)
Nursing	0.00	8.19 \pm 28.4 (3.5)	0.00	18.15 \pm 33.7 (1.9)	0.00	4.78 \pm 19.4 (4.6)
Foraging	60.24 \pm 22.8 (0.4)	93.28 \pm 41.6 (0.4)	6.46 \pm 21.7 (3.4)	0.54 \pm 1.9 (3.6)	17.27 \pm 40.5 (2.3)	31.93 \pm 44.9 (1.4)
Lunging	0.33 \pm 0.5 (1.5)	0.17 \pm 0.4 (2.3)	0.29 \pm 0.5 (1.6)	0.00	0.13 \pm 0.3 (2.7)	0.19 \pm 0.4 (2.1)
Chasing	1.00 \pm 1.4 (1.4)	0.27 \pm 0.5 (1.8)	0.29 \pm 0.7 (2.3)	0.65 \pm 0.9 (1.4)	0.13 \pm 0.5 (4.0)	0.44 \pm 0.9 (2.1)
Fleeing	0.86 \pm 0.9 (1.1)	0.87 \pm 1.1 (1.3)	1.08 \pm 1.6 (1.5)	0.46 \pm 0.8 (1.7)	0.60 \pm 1.1 (8.4)	0.78 \pm 1.2 (1.5)
Grappling	0.00	0.00	0.21 \pm 0.5 (2.3)	0.15 \pm 0.4 (2.4)	1.71 \pm 2.5 (1.5)	0.47 \pm 1.4 (2.9)
Curve-body	0.00	0.75 \pm 2.6 (3.5)	0.00	0.00	0.00	0.13 \pm 1.1 (8.4)
Submit	0.00	0.00	0.00	0.15 \pm 0.6 (3.6)	0.13 \pm 0.5 (4.0)	0.06 \pm 0.3 (5.9)
Follow	0.63 \pm 1.2 (1.9)	0.00	1.97 \pm 3.1 (1.6)	0.00	0.00	0.59 \pm 1.8 (3.0)
Followed	0.00	0.29 \pm 1.0 (3.5)	0.00	1.67 \pm 4.1 (2.5)	0.93 \pm 2.0 (2.1)	0.57 \pm 2.1 (3.6)
Tail-up	0.00	0.29 \pm 0.8 (2.6)	0.00	0.92 \pm 3.3 (3.6)	0.00	0.22 \pm 1.5 (6.6)
Repulsed	0.00	0.00	0.00	0.00	0.00	0.00
Mounting	0.08 \pm 0.3 (3.5)	0.00	0.31 \pm 0.8 (2.5)	0.00	0.22 \pm 0.6 (2.8)	0.14 \pm 0.5 (3.6)

Table 12.—Continued.

Variable	Group					Total
	<i>Galea</i> males	<i>Galea</i> females	<i>Kerodon</i> males	<i>Kerodon</i> females	<i>Kerodon</i> juveniles	
Crawl-over	2.63 ± 9.1 (3.5)	0.00	0.00	0.69 ± 1.6 (2.3)	1.82 ± 3.3 (1.8)	0.99 ± 4.1 (4.1)
Allogrooming	0.00	0.00	0.00	1.43 ± 5.2 (3.6)	0.00	0.27 ± 2.2 (8.4)
Scentmarking	0.00	0.00	0.56 ± 2.3 (4.1)	0.00	0.00	0.14 ± 1.1 (8.4)
Activity-ratio	0.59 ± 0.2 (0.4)	0.58 ± 0.3 (0.5)	0.08 ± 0.1 (1.2)	0.11 ± 0.2 (1.5)	0.14 ± 0.1 (1.0)	0.28 ± 0.3 (1.1)

separating groups than a simultaneous analysis of all variables. The five populations therefore were subjected to a multiple stepwise discriminant analysis (Table 14) to determine which linear combinations of variables were most effective in separating the groups. In addition, each sample was assigned a probability of classification to each of the five populations.

The only variable not included in the multiple stepwise D.A. was "repulsed." All others were incorporated in the construction of the discriminant functions. For the analysis of the five-group data, there were three significant orthogonal axes (Table 15). The standardized discriminant function coefficients (Table 16) for these three axes indicate the relative position and importance of all the variables used in forming the discriminant functions. A two dimensional scattergram illustrates the relative po-

sitions of the group centroids and all individual samples. As there were three significant axes (explaining 96.3% of the total dispersion), the relative positions of the five-group centroids can be visualized much more clearly in three dimensional space (Fig. 36). Discriminant Function I separates the *Galea* groups from *Kerodon*. Four variables are heavily weighted on the *Galea* side of the axis—activity-ratio; sit ground; foraging; sandbathing. The variables most heavily weighted on the *Kerodon* side of the axis include nursing, suckling, climbing, grappling, scentmarking, fleeing, submit, mounting, and sit rocks.

The variables, which were important in separating the genera, corresponded fairly closely to the univariate results (Fig. 35); however, discriminant analysis was more sensitive in detecting other biologically important differences between groups.

Table 13.—Results of a Kruskal-Wallis one-way analysis of variance by ranks for all five groups, *Kerodon* and *Galea* adults, and *Kerodon* adults and juveniles. The Kruskal-Wallis test statistic (*H*) and the level of significance (*P*) are presented. All variables with $P < 0.05$ are considered significant.

Variable	Groups compared					
	All five groups		Four adult groups		Three <i>Kerodon</i> groups	
	<i>H</i>	<i>P</i>	<i>H</i>	<i>P</i>	<i>H</i>	<i>P</i>
Inactive	22.59	.0002	8.12	.0436	19.73	.0001
Sit Rocks	35.29	.0000	29.20	.0000	—	—
Sit Ground	26.25	.0000	17.91	.0005	—	—
Sit Trees	35.79	.0000	30.65	.0000	15.23	.0005
Sit Sand	23.82	.0001	16.96	.0007	—	—
Climb	25.67	.0000	23.95	.0000	6.68	.0355
Walk	14.30	.0064	13.17	.0043	—	—
Suckle	25.78	.0000	—	—	15.01	.0006
Nurse	14.01	.0073	9.72	.0211	10.85	.0044
Forage	46.06	.0000	41.44	.0000	—	—
Grapple	14.67	.0054	—	—	6.10	.0473
Follow	15.33	.0041	9.97	.0189	11.44	.0033
Crawl-over	12.51	.0139	—	—	7.52	.0233
Activity-ratio	39.25	.0000	33.58	.0000	—	—

Table 14.—Wilk's lambda (*U*-statistic), univariate *F*-ratio, and level of significance (*P*) for all 28 variables used in the discriminant analysis. *P*-value is for the *F*-statistic with 4 and 65 degrees of freedom. There were 10 significant variables for the five-group comparison.

Variable	Wilk's lambda	F	P
Inactive	0.92	1.36	>.25
Sit rocks	0.78	4.35	<.005
Sit ground	0.78	4.33	<.005
Sit trees	0.89	1.98	>.10
Sit sand	0.77	4.62	<.005
Running	0.97	0.48	>.50
Climbing	0.75	5.26	<.005
Walking	0.82	3.34	<.025
Sandbathing	0.94	0.97	>.25
Grooming	0.94	0.98	>.25
Suckling	0.77	4.61	<.005
Nursing	0.86	2.52	=.05
Foraging	0.40	23.44	<.001
Lunging	0.90	1.64	>.10
Chasing	0.87	2.28	>.05
Fleeing	0.96	0.62	>.50
Grappling	0.75	5.34	<.001
Curve-body	0.93	1.22	>.25
Submit	0.95	0.71	>.50
Follow	0.78	4.42	<.005
Followed	0.90	1.68	>.10
Tail-up	0.94	1.01	>.25
Repulsed	1.00	0.00	>.75
Mounting	0.93	1.12	>.25
Crawl-over	0.93	1.07	>.25
Allogrooming	0.93	1.10	>.25
Scentmarking	0.95	0.76	>.50
Activity-ratio	0.38	26.01	<.001

Sandbathing was indicated as an important variable in separating the *Galea* population from *Kerodon*; qualitative observations had also indicated this to be true. Grappling was indicated as an important gesture in characterizing the *Kerodon* ethogram. This is another difference which was not detected by the non-parametric multiple comparisons test. Fleeing was also heavily weighted for *Kerodon*, primarily because of the relatively long extended

Table 15.—The three significant discriminant functions extracted for the five-group comparison and associated statistics.

Statistics	Discriminant function		
	I	II	III
Percent variance	83.45	6.69	6.14
Wilk's lambda	0.0043	0.0878	0.2231
Chi-square	288.269	128.916	79.511
DF	108	78	50
Significance level	0.001	0.001	0.005

Table 16.—Standardized discriminant function coefficients for the 27 experimental variables on the first three discriminant axes. The sign and numerical value of the coefficient indicate its relative position and relative importance on the axis. Variable number 23, repulsed, was not included in the formation of the axes.

Variables	Standardized discriminant function coefficients		
	Function I	Function II	Function III
Inactive	-0.037	-0.246	0.170
Sit rocks	-0.091	-0.255	0.256
Sit ground	0.291	-0.187	0.107
Sit trees	0.051	0.017	0.263
Sit sand	0.040	-0.000	0.366
Running	0.024	0.011	-0.094
Climbing	-0.181	-0.181	0.201
Walking	0.087	-0.223	-0.004
Sandbathing	0.141	0.087	-0.492
Grooming	0.071	0.510	-0.129
Suckling	-0.181	-0.292	-0.379
Nursing	-0.217	-0.845	0.704
Foraging	0.098	-0.627	-0.433
Lunging	0.021	0.337	0.081
Chasing	0.022	-0.128	0.332
Fleeing	-0.139	0.078	-0.108
Grappling	-0.174	-0.200	-0.302
Curve-body	-0.007	0.296	-0.213
Submit	-0.133	0.079	0.179
Follow	0.036	0.541	0.173
Followed	-0.068	-0.514	0.034
Tail-up	0.024	0.277	0.156
Mounting	-0.127	0.087	-0.150
Crawl-over	-0.031	0.030	-0.020
Allogrooming	-0.027	0.268	-0.320
Scentmarking	-0.152	-0.041	0.035
Activity-ratio	0.590	0.211	0.468

chases when the fleeing animal weaved in and out of the rocks.

The small sample size did generate some spurious results, however. Submit and mounting were both heavily weighted for *Kerodon*. Nonquantified observations indicated an approximately equal frequency of occurrence of these traits for the two genera. Scentmarking was observed only once in 70 trials, and was one of the three observations collected for *Kerodon* in 2 years of study. Scentmarking was actually far more common in *Galea*.

Discriminant Function II separates the males from the female-juvenile complex. The males are weighted most heavily by grooming, lunging, and following, whereas the most important variables on the female side include nursing, foraging, and followed. The third axis is somewhat confused, but serves primarily to separate *Kerodon* and *Galea* females from *Kerodon* juveniles. Nursing and ac-

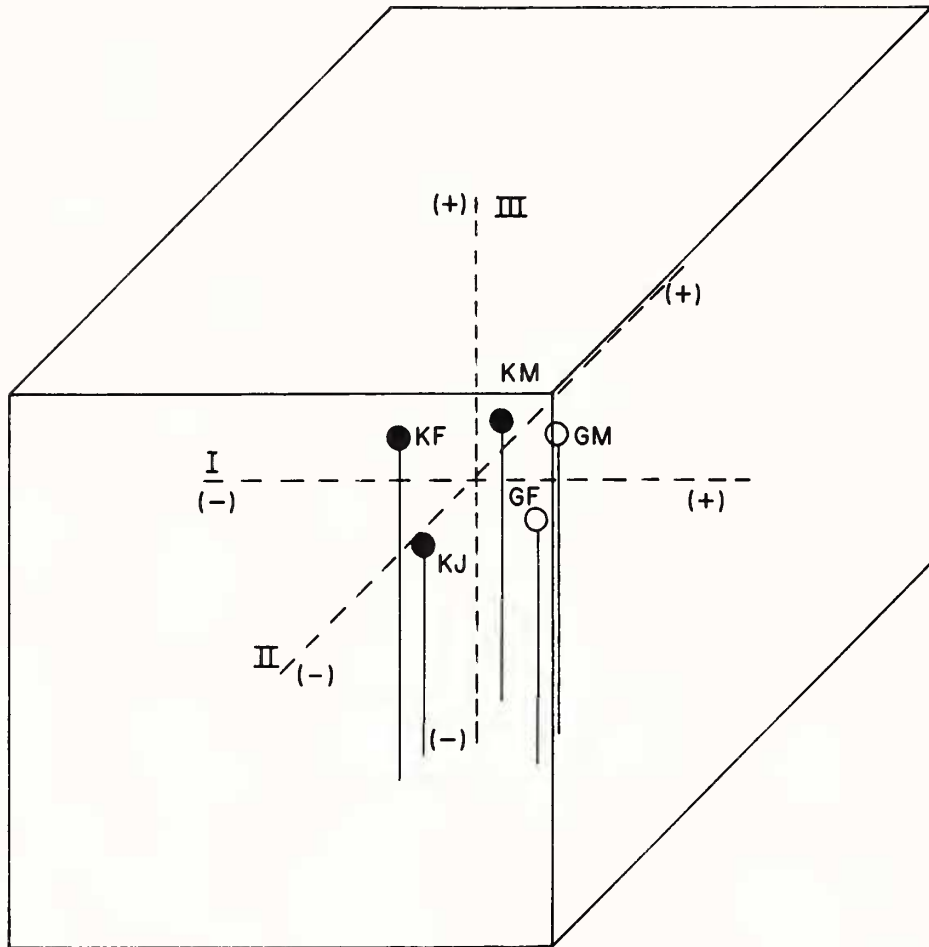


Fig. 36.—Five-group centroids in three dimensional space. Dotted lines represent the three significant discriminant functions, which intersect at zero.

tivity ratio are heavily weighted for the adults's side. Suckling is one of the more important variables on the juvenile side; however, sandbathing and foraging are more heavily weighted. A great deal of this is due to the intermediate position on this axis of *Galea* females, between *Kerodon* females and juveniles.

The results of the classification procedure indicate that all samples were correctly classified by genus (Table 17). There were some misclassifications by sex or age; however, the percent of cases correctly classified was 84.3. One of the misclassified juveniles was a "borderline" case, a juvenile male already presenting a few adult characteristics. This particular juvenile was given a 56.9% probability of being an adult male and a 42.5% probability of being a juvenile . . . exactly what one might expect for a maturing animal.

As juvenile behavior was extremely variable, an additional discriminant analysis was run using only the four adult groups to determine if a more efficient classification could be obtained. As expected, there were only two significant axes and the important discriminant function coefficients remained basically the same. The scattergram and relative group centroid distances were also very similar to the five group analysis. The percent of correctly predicted group memberships, however, was much higher (90.7) when juveniles were eliminated from the analysis.

All five groups analyzed represent relatively homogeneous populations based on mean durations. The four adult groups were especially consistent. A compound variable, like the *mean population duration*, seems to facilitate group separation and classification of individual samples. It is also more

Table 17.—Results of the SPSS Discriminant classification procedure. No samples were misclassified by genus, however there were 15.71% misclassifications by age or sex.

Actual group	No. of cases	Predicted group membership				
		Group 1	Group 2	Group 3	Group 4	Group 5
Group 1 <i>Galea</i> males	12	11 91.7%	1 8.3%	0 0.0%	0 0.0%	0 0.0%
Group 2 <i>Galea</i> females	12	2 16.7%	10 83.3%	0 0.0%	0 0.0%	0 0.0%
Group 3 <i>Kerodon</i> males	17	0 0.0%	0 0.0%	16 94.1%	1 5.9%	0 0.0%
Group 4 <i>Kerodon</i> females	13	0 0.0%	0 0.0%	2 15.4%	10 76.9%	1 7.7%
Group 5 <i>Kerodon</i> juveniles	16	0 0.0%	0 0.0%	2 12.5%	2 12.5%	12 75.0%

difficult to interpret. A variable which is significantly different between populations may be larger or smaller, it may be more common or more infrequent or it may differ because of combinations of the above. The ideal situation would be to analyze each variable in a variety of ways. For the purposes of characterizing group differences and classifying individual samples, however, frequency weighted mean durations proved very effective. When univariate methods were used to analyze the data, the groups were difficult to distinguish. When all variables were analyzed simultaneously all five groups were separated, and 85% of the individual trials were correctly classified. The use of quantified aspects of a species' behavioral repertoire (frequency weighted mean durations in this case) as a system of measurement was extremely effective in clarifying group differences. This was especially effective considering the sample sizes.

Principal components analysis was run on three groups—*Kerodon* males; *Kerodon* females; and *Galea* adults. Initial factors were extracted by the principal components method of the BMDP package (Niè et al., 1975) from a correlation matrix with all diagonal elements set at one. Only factors that explained 10% or more of the total variance were used in the interpretation of the results. In order to facilitate interpretation, the factor matrix was rotated to obtain a simpler structure via a Kaiser Normal Varimax rotation. The rotated factor loadings were then sorted. The zero factor loading was set at 0.2500.

Five factors in the *Galea* population accounted for 10% (or more) of the total variance. None of the factors, however, are especially strong; in fact, the

total variance accounted for by all five factors is only 58%. The most interesting factor, II, tends to separate submissive animals from dominant animals. Factors I and V separate out two specific single samples, Factor III separates the dominant female from other animals and Factor IV distinguishes males following estrous females from the rest of the population.

The results obtained for *Kerodon* are more enlightening. There were five factors selected for *Ker-*

Table 18.—Factor loading matrix for *Kerodon* males. The matrix has been rearranged so that columns are in order of percent variance explained. The rows also were rearranged, so that for each successive factor, loadings greater than 0.500 appear first. The zero factor loading has been set equal to 0.250.

Variable	No.	Factors				
		I	II	III	IV	V
Foraging	9	0.98	0.00	0.00	0.00	0.00
Scentmarking	16	0.97	0.00	0.00	0.00	0.00
Activity-ratio	17	0.96	0.00	0.00	0.00	0.00
Walking	7	0.92	0.28	0.00	0.00	0.00
Fleeing	12	0.30	0.88	0.00	0.00	0.00
Sit ground	3	0.00	0.82	0.00	-0.31	0.00
Grappling	13	0.00	0.80	0.00	0.46	0.00
Follow	14	0.56	0.65	0.00	0.36	0.00
Running	5	0.00	0.00	0.89	0.00	0.00
Lunging	10	0.00	0.00	0.83	0.00	0.00
Inactive	1	0.00	0.00	0.00	0.70	0.00
Climbing	6	0.40	0.00	0.00	-0.67	0.00
Chasing	11	0.00	0.00	0.42	0.55	0.00
Sit rocks	2	0.00	0.00	0.00	0.00	0.90
Grooming	8	0.46	0.00	-0.28	-0.27	0.71
Sit trees	4	-0.25	0.00	-0.50	0.00	-0.59
Mounting	15	0.00	0.00	0.00	0.00	0.00
Eigenvalue		4.69	2.88	2.13	1.89	1.75
Percent variance		27.6	17.0	12.5	11.1	10.3

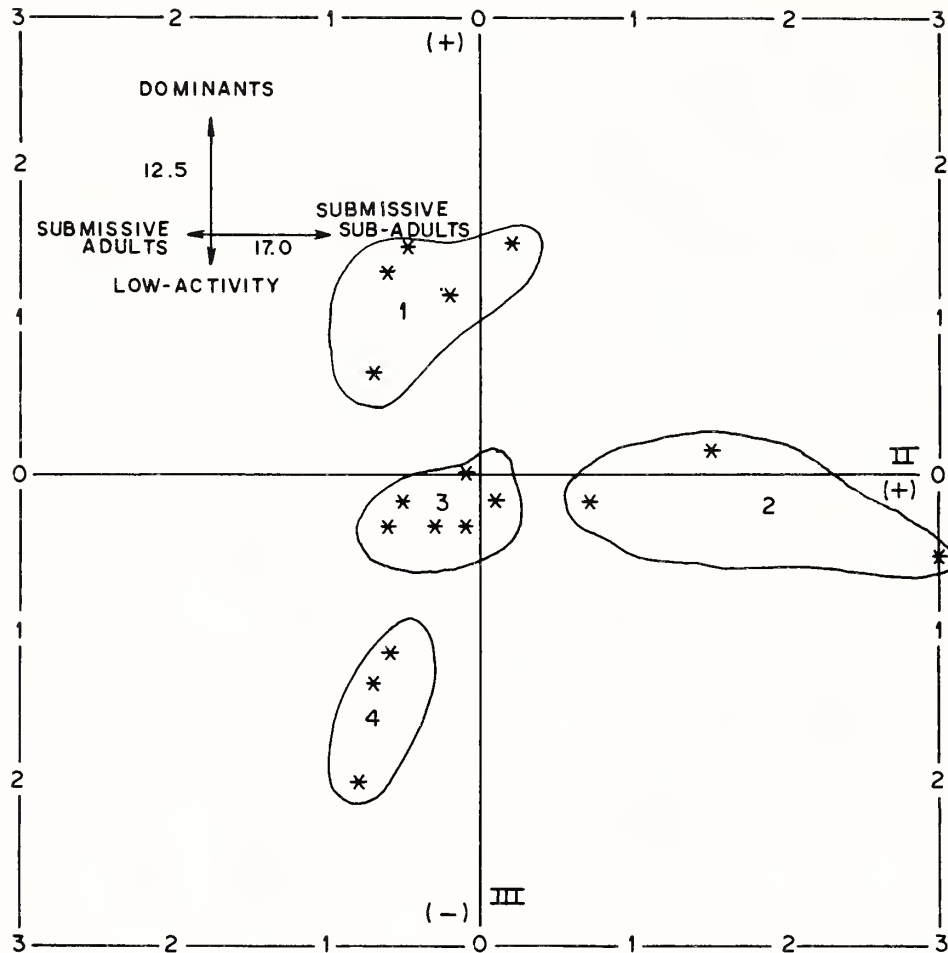


Fig. 37.—Graph of factor scores for *Kerodon* males in relation to factors II and III. Small graph in upper left hand corner indicates the percent variance accounted for by each factor, as well as the behavioral component of the factor. Five of the seven trial runs on the number one and two males are enclosed in area one. Area two represents subadult males; individuals which were submissive and maintained a juvenile characteristic (grappling). Area three, near the origin, represents submissive adult males. Area four contains three trials in which animals did nothing but sit, either in the rocks or in the trees, for nearly the duration of the trials.

odon males (Table 18), accounting for 78.5% of the total variance. Factors I, IV and V separated single trials from the rest of the population. Factor II distinguished obviously submissive males from other males, and Factor III separated actively dominant males from animals which spent little, if any, time active. A plot of the factor scores for each trial on these two axes give a good separation of dominant and submissive individuals (Fig. 37).

Results for *Kerodon* females indicated six factors which accounted for 10% or more of the total variance. Factor I distinguished behaviors associated with nursing females from other animals. Factor II separated estrous females from non-estrous fe-

males. Factors II through VI again separated individual trials from the rest of the population. The relatively small sample size used (13 to 24) is the reason for the frequent occurrence of this phenomenon. Factor analyses are most effective with large sample sizes, although the minimum allowable sample size is unknown (Frey and Pimentel, 1978). Nevertheless there was some consistency in the results. Factors of biological coherence which explained 10% or more of the variance always keyed on one of four things: gestures associated with dominance; gestures associated with submissiveness; estrous females (and associated behaviors); and nursing females.

DISCUSSION

EVOLUTION OF BEHAVIOR IN THE CAVIIDAE

The evolution of morphological and behavioral differences in the family Caviidae is strongly linked to the different habitat requirements of the six genera. In order to attempt a reconstruction of the evolutionary trends within this family, it is necessary to envision a caviid prototype, one from which the living genera could have been derived. Rood (1972) considered *Microcavia* to be most similar to the caviine ancestor. This genus has a relatively high social tolerance, amicable relationship among females, simplified sexual and reproductive repertoire, and occupies open thorn-bush formations. This description is similar to what might be expected for the caviid prototype, an animal that possessed what was termed by Eisenberg (1963), a "loose social system."

This caviid prototype first appeared in South America in the mid-Miocene, and by late Miocene both subfamilies were present (Pascual, 1962). All caviids show a reduction in the number of toes on the hindfoot, indicating that at one point in their evolutionary history, they were moderately digitigrade and cursorial. Although the actual foot posture and mode of locomotion now varies greatly among the genera, this basic foot form remains constant within the family. It is possible that changing selective pressures have caused the caviids to become secondarily small and less cursorial than their precursors.

There are some major morphological and behavioral differences between the subfamilies. The Dolichotinae evolved in high plains, desert, and open grasslands; their extensive morphological adaptations for a cursorial life were described in detail by Dubost and Genest (1974). In occupying this open, structurally homogeneous habitat, it became increasingly difficult for the female to protect and care for the young alone, and selection subsequently favored a more active participation by the male in protecting the female and young from predators. Males would already have been tolerated by the female during and after parturition in the "loose social system" ancestor, thus no extensive modifications in the social system were necessary. Sexual patterns remained relatively simple. Basic hystricomorph gestures like enurination and the tail-up are present, and males display a figure-eight passing

behavior to the female during courtship. This gesture may well have been part of the repertoire of the caviid ancestor as it is also present in *Cavia* (prowl) and in a modified form in *Kerodon* (circling). Aggressive behavior in *Dolichotis* is also fairly simple, consisting of approaches, lunges, chases with rump biting, and a mouth-to-mouth threat posture (Dubost and Genest, 1974).

In the caviines, *Microcavia* maintains many similarities to the hypothetical caviine ancestor. The presence of limited shelter sites may have been an important factor in favoring the maintenance of low aggressive levels in *Microcavia*, particularly among females.

Galea and *Cavia*, respectively, occupy increasingly more productive and diverse habitats (scrub forest, cerrado, pampas) offering an abundance of shelter, food, and other resources. Although more productive than the thorn-bush associations occupied by *Microcavia*, these habitats remain structurally relatively homogeneous. Where such habitats occur, single individuals would not be able to monopolize clumps of resources without large expenditures of time and energy. Individuals within populations would thus tend to be dispersed rather than clumped. Selection would favor the development of territoriality, effective aggressive gestures, and complex displays for the attraction of females. More effective means of visual, vocal, or olfactory communication would also be favored. The end result would be a decrease in social tolerance within the population and an increase in the complexity of behavioral repertoires. *Galea*, and to a greater extent *Cavia*, seem to have evolved under these types of selective pressures.

Kerodon, however, deviates markedly from this caviine trend. It does occupy a relatively productive habitat; however, resources (rock piles) are highly clumped. Thus it becomes quite feasible, in terms of time and energy, for a single animal (most likely a male) to monopolize a large amount of resources critical to other animals (most likely females). This is a situation with a high potential for the evolution of a harem-based mating system (Emlen and Oring, 1977) requiring social tolerances within resource clumps and complex aggressive gestures to protect the clumps from intruders.

Kerodon was probably derived from a *Kerodon*-

Galea prototype which inhabited northeastern and central Brazil, the area which is now covered by the Cerrado-Caatinga complex. The Quaternary in South America was dominated by alternations between wetter and drier periods (Vanzolini, 1970; Vuilleumier, 1971) and the importance of these climatic conditions in speciation in the Amazonian fauna has previously been reported by various authors (Haffer, 1969; Vanzolini and Williams, 1970; Brown et al., 1974). It is quite possible that they were also of importance in northeastern Brazil. Geomorphological data indicate that the Caatinga and Cerrado vegetation types expanded into the Amazon Basin during dry periods (Vanzolini, 1973), and populations of the *Kerodon-Galea* prototype could have been isolated in the rocky chains of hills and plateaus in northeastern Brazil during a pronounced drought. These hills and plateaus are more humid than the Caatinga lowlands, and many receive orographic rainfall (Markham, 1972). The plateaus currently serve as refugia in the dry Caatinga for a number of more mesic-adapted species (for example, *Tamandua tetradactyla*) and may have been important refugia for mammals during the Quaternary. Populations restricted to the more mesic plateaus (*Kerodon* precursors) would have diverged from the main body of the populations (*Galea* precursors) which was pushed southward or eastward; Brown et al. (1974) have postulated a large mesic refuge on the southeastern coast of Brazil. As the plateau chains are fairly rocky, animals isolated there would be expected to have evolved the complex morphological and behavioral features necessary for the successful exploitation of this habitat. The *Galea* precursors, which migrated southward with the refugia, would have changed little morphologically or behaviorally, as they would have experienced a minimal change in habitat. A return to more mesic conditions allowed for the recolonization of the lowland areas by the main population (*Galea*), which probably maintained a strong morphological resemblance to the initial prototype. This would result in the current situation; two closely related sympatric genera (Pascual, 1962), one of which shows morphological and behavioral adaptations to exploit rocky habitats (*Kerodon*) and the other occupies the lowland areas and shows morphological and behavioral similarities to the basic caviine form (*Galea*). A discussion of the major differences between these two genera and the ecological factors which may have shaped these differences follows.

TRENDS IN BEHAVIORAL EVOLUTION

Eisenberg's (1963) study on the comparative behavior of heteromyid rodents provided valuable insights on the evolution of social behavior within the family. The data presented here allow a preliminary evaluation of the trend in evolution of social behavior within the family Caviidae. Rood (1972) furnished both field and colony observations on *Cavia*, *Microcavia*, and *Galea musteloides*. *Dolichotis* was studied under seminatural field conditions in France (Dubost and Genest, 1974) and behavioral data on *Pediolagus* was reported by Eisenberg (1974), Kleiman (1974), and Wilson and Kleiman (1974). Behavioral information available on the dolichotines is somewhat sketchy and primarily descriptive. Because of the fine study on the Argentine caviines, however, the patterns of ecology and behavior in the subfamily Caviinae can be examined in some detail (Table 19). *Galea spixii* and *G. musteloides* are, in general, fairly similar. A few traits observed by Rood (1972) were not observed in *G. spixii*. Rearing, a common gesture in *G. musteloides*, was completely absent in *G. spixii*. Climbing and digging were not observed for *G. spixii*, but both gestures were probably associated with the chicken wire outdoor enclosures used by Rood. The kiss was observed for *G. spixii*; however, it was extremely rare. Two other aggressive gestures (jump-turns and the submissive crouch) were very common in *G. spixii* but were not observed in *G. musteloides*. There are thus three important gestural differences at the species level—rearing, jump-turns, and the submissive crouch.

Kerodon has by far the most complex overall repertoire among the caviine genera, especially in relation to contactual, aggressive, and sexual postures. *Kerodon* vocalizations are also quite complex. Rood suggested a trend in complexity among the Argentine caviines, with *Microcavia* being the least complex in terms of behavioral interactions, and *Cavia* the most complex. If *Kerodon* is considered on the same basis, it is far more complex than *Cavia*. *Kerodon* possesses nearly all of the gestures present in the other genera, and in addition has a complex contact-promoting play behavior (grappling), a stereotyped aggressive gesture (jousting), and two specialized reproductive displays (circling and foot tapping). Also, the alarm whistle is a complex vocal display with an apparent social function.

Rood (1972) also concluded that the three genera of Argentine caviines differ in their degree of social

tolerance. *Cavia* was considered a distance animal, with a diverse aggressive repertoire and a sparse repertoire of contact-promoting gestures. *Microcavia* was considered the most social of the two genera, and this sociality is reflected in the complex array of contactual gestures, and a correspondingly simple aggressive repertoire.

Kerodon has both a complex aggressive behavior and diverse contactual postures. This contradictory situation is related to the maintenance of harems. A great diversity of contactual gestures exists within the harem to reduce aggression and maintain a high level of communication among harem members. There also exists a complex aggressive repertoire to ritualize aggressive interactions between females and juveniles within the harem, thus reducing potentially crippling encounters, and to protect the rocks from invasion by outsiders. *Kerodon* represents a major divergence from the typical caviid trend of straight line dominance relationships. This divergence is related to the distinctly different habitat type occupied by this genus.

Vocalizations of the two genera maintained the relative stereotypy of hystricomorph sounds noted by Eisenberg (1974). In his study, the vocalizations of a number of hystricomorph rodents were examined and classified according to their functional context. Using Eisenberg's data and classifications, I compared *Kerodon* and *Galea spixii* vocalizations with those of a number of other caviid species (Table 20).

Galea spixii possesses almost the same vocal repertoire as *G. musteloides*, one exception being the ambiguous function of the tooth chatter. Tooth chatters were given by *G. spixii* individuals in a variety of aggressive contexts and were always given by the more subordinate individual in a given encounter.

The slow whistle and alarm whistle are unique to *Kerodon*, *Dasyprocta punctata* gives an alarm bark (Smythe, 1978), and *Dolichotis patagonum* emits a sharp "wheet" (Eisenberg, 1974). *Octodon degus* uses a sharp squeak, at least part of which is repeated (Eisenberg, 1974). Both *Spalacopus* and *Lagidium* give what appear to be warning calls, of a very pure harmonic quality, although little is known of their function in the wild. *Lagidium* inhabits rock piles similar to *Kerodon* habitat, and the call in this genus may have the same function as is described here for *Kerodon*. No other hystricomorph has been reported to give a repeated, high-pitched whistle like *Kerodon*'s.

Table 19.—Comparison of the relative frequencies of occurrence of selected behavioral traits among five species of caviines. 0 = absent, 1 = rare, 2 = common. Based on Rood (1972).

Behavior	<i>Microcavia</i>	<i>Cavia</i>	<i>Galea musteloides</i>	<i>Galea spixii</i>	<i>Kerodon</i>
Maintenance behavior					
Climbing	2	1	1	0	2
Nosing	2	2	0	2	2
Combing	2	2	0	0	2
Rolling (Sandbathing)	2	1	2	2	0
Digging	2	1	1	0	0
Upright attend	2	1	1	1	2
Swimming	0	1	0	0	0
Frisky hops	2	2	2	1	2
Scentmarking	2	2	2	2	1
Contactual behavior					
Climb-over (Crawl-over)	2	1	1	1	2
Side-sit	2	0	2	2	1
Rear-sit	2	0	2	1	1
Kiss	2	0	0	1	2
Social grooming	2	2	2	1	2
Grappling	0	0	0	0	2
Agonistic behavior					
Jump turn	1	0	0	2	2
Stand threat	0	2	2	1	1
Tail-up	0	2	2	2	2
Facing	2	2	0	0	1*
Kick-back	1	1	0	0	0
Head-up	0	2	0	0	0
Submit	2	0	0	2	2
Jousting	0	0	0	0	2
Reproductive behavior					
Rearing	0	0	2	0	0
Riding	2	2	0	0	2
Rumba	0	2	0	0	0
Rumping	0	2	0	0	0
Circling	0	1*	0	0	2
Foot tapping	1*	0	0	0	1

*Notes: *Microcavia* males tap the rump of females. *Cavia* exhibit the *prowl*, a gesture which superficially resembles circling. *Kerodon* juveniles exhibit a gesture similar to facing while grappling.

The alarm whistle is interesting in that it resembles a true alarm call. At the approach of a predator, an animal will sit upright and begin to whistle. The predator is probably detected by sound or smell, as the whistling starts while it is still some distance away. Other animals will respond to the whistle by assuming the upright attend position. The animals remain upright until the intruder is first seen by one of the animals, at which time they all flee.

My impression is that the first individual which detects the approach of a predator gives the alarm whistle, alerting the other animals. All animals then assume the upright position, and begin to watch for the predator. The initial "whistler" would probably

Table 20.—Contextual classifications of various vocalizations present in the Caviidae. Data and classifications are from Eisenberg (1974) and this study. Code: Roman numerals = syllable types (see reference above for detailed descriptions of sonogram analysis), a = ascending frequency, d = descending frequency, ad = complex frequency modulation, s = short syllable, l = long syllable, r = repeated emission, and u = no appropriate frequency modulation.

Species	Warning sounds					
	When started	When threatening (to a conspecific or slow predator)	Before or after attack	Avoiding while being approached	When injured	When defeated
<i>Dolichotis patagonum</i> (Eisenberg, 1974)	sharp wheet	tooth chatter III; grunt		long wheet with grunt		
<i>Pediolagus salinicola</i> (Eisenberg, 1974)		whine				
<i>Cavia porcellus</i> (Eisenberg, 1974)	tutt-tutt II s, r	tooth chatter III r	grunt, snort	low wheet I a d, s, r	sharp squeak	squeal II l
<i>Cavia aperea</i> (Rood, 1972)		tooth chatter III	grunt	bubbly squeak		squeal
<i>Microcavia australis</i> (Rood, 1972)	tsit	tooth chatter III				
<i>Galea musteloides</i> (Rood, 1972)		tooth chatter III; drumming	stutter			
<i>Galea spixii</i> (this study)		drumming; tooth chatter	stutter; bark; tooth chatter	peepy squeaks	squeak	squeak; tooth chatter
<i>Kerodon rupestris</i> (this study)	alarm whistle I r s				squeal II a d	

Table 20.—Continued.

Species	When calling young (?)	When being groomed	When following	When seeking contact	When courting	Special contexts
<i>Dolichotis patagonum</i> (Eisenberg, 1974)		short grunts	cluck II a d, s	wheet I a d, l		
<i>Pediolagus salinicola</i> (Eisenberg, 1974)			cluck	wheet		
<i>Cavia porcellus</i> (Eisenberg, 1974)	cluck II a d	gurgle; short II a d	clucks II a d, s	wheet I a d, s	purr II u s; r	inflected wheets
<i>Cavia aperea</i> (Rood, 1972)					rumble	
<i>Microcavia australis</i> (Rood, 1972)					rumble	
<i>Galea musteloides</i> (Rood, 1972)					churr	
<i>Galea spixii</i> (this study)				peepy squeaks (juv.)		
<i>Kerodon rupestris</i> (this study)				peepy squeaks		slow whistle; churr; tooth chatter (all anxiety)

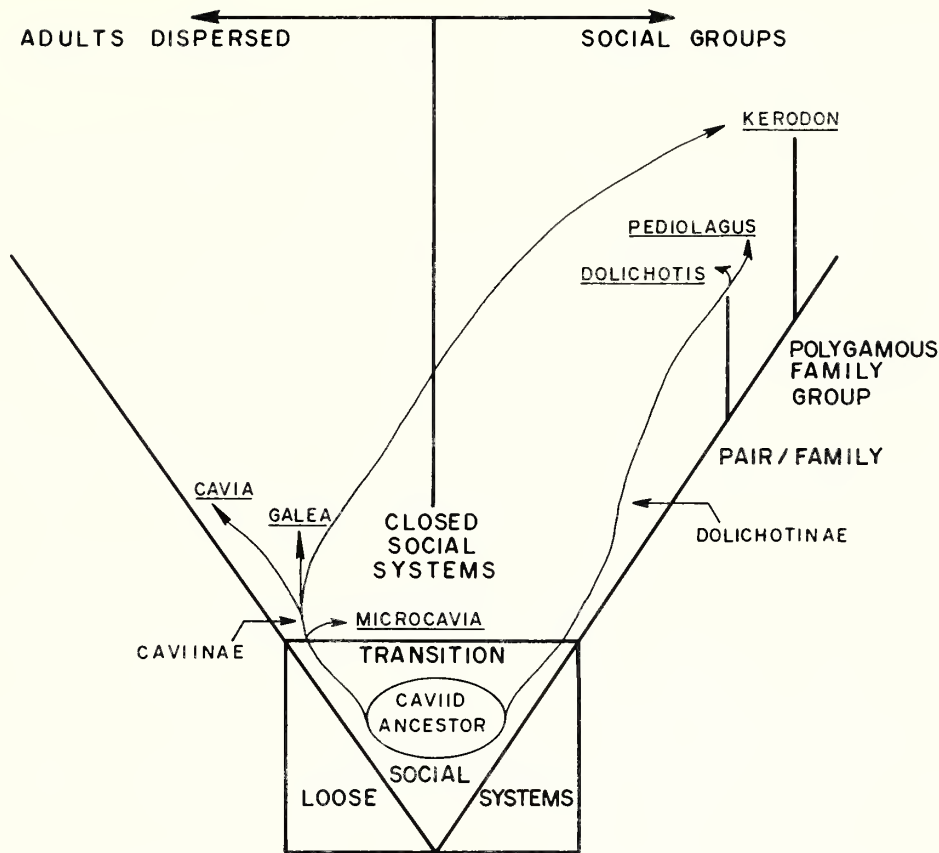


Fig. 38.—A hypothetical representation of the trend in evolution of social behavior in the family Caviidae based on Eisenberg's (1963) model for the classification of steps in the evolution of rodent social systems. The thin line illustrates the trend in behavioral evolution for the six genera in the family, and does not indicate phylogenetic affinities. *Microcavia* approximates the transitional social system, that is, showing trends towards dispersion as adults while maintaining a reasonable level of social tolerance. Environmental variables were more important than phylogenetic constraints (for example, subfamily) in determining trends in the Caviidae.

not place himself in immediate danger, because at the time of detection the predator is still distant. A greater danger would be to flee without any idea of the direction from which the predator is approaching. This is especially true in the rugged, boulder-strewn areas which *Kerodon* inhabit, because visual contact may not be established until the predator is quite close. By alerting other animals in the population, the "whistler" would gain the advantage of having numerous other eyes scanning the pits and depressions for an approaching predator. Once an individual sees the predator and flees, the rest of the population does likewise. All individuals gain the same advantage, and are exposed to little individual risk. Indeed, indiscriminate fleeing may well be far more risky than maintaining an alert position on top of a boulder.

The resemblance of the alarm whistle to the squeal (distress, pain) and the slow whistle (anxiety, stress) aids in the development of a model for the evolution of such an alarm call followed by the "alert" reaction. Animals which initially gave a distress squeal upon hearing an approaching predator would have gained the benefit of observing the response of other animals to the squeal. Individuals which did *not* respond to the squeal, or which fled indiscriminately, would more likely have been lost to predators; thus individuals which assume an alert position would have been favored. Animals which gave a "better" squeal, therefore alerting (and consequently observing) more individuals, would also have been favored, the end result being the modifications of the distress squeal into a penetrating whistle capable of alerting the maximum number of

individuals. If this were the case, the alarm whistle should still maintain a relation to its initial, basic function; that of a distress call. This is apparently true, for as an animal is cornered it will give the whistle.

Various authors have suggested that alarm calls may actually benefit the caller (Trivers, 1971; Charnov and Krebs, 1975; Wilson, 1975; Sherman, 1977; Staton, 1978) either directly, or indirectly by increasing the caller's inclusive fitness (Hamilton, 1964). By explaining the *Kerodon* whistle in the most parsimonious way possible, I have concluded that the call could have evolved through natural selection acting on the individual by conferring a direct benefit on the caller. Emlen (1973) has stated that one of the important functions of kin selection, however, may be in enhancing selection at the individual level. As *Kerodon* occur in semi-isolated rock piles, living in groups of related individuals (see below), the rate of selection of the alarm call might have been greatly accelerated by a kin effect.

A proposed model for the evolution of caviid social behavior can be graphically represented in terms of Eisenberg's hypothetical model (Fig. 38). The differing social organizations present for each genus, considered in relation to its habitat requirements, offer an example of the importance of social behavior in ecological adaptation.

MATING SYSTEMS

Orians (1969), in a discussion of the evolution of mating systems, indicated a number of characteristics of the biology of birds and mammals which would favor a polygynous breeding system. Among these were precocious young, limited nesting sites, and juvenile survivorship, which is little influenced by paternal care.

Emlen and Oring (1977) classified monogamous and polygamous mating systems on the basis of certain ecological criteria. The environmental potential for polygamy (EPP) was viewed as dependent upon three factors—the spatial distribution of resources; the temporal distribution of sexually receptive mates; and the operational sex ratio, defined as "the average ratio of fertilizable females to sexually active males at any given time."

When resources are clumped, they can be monopolized more easily by a single individual. A small proportion of the population can thus control a large proportion of the available resources. If these resources are necessary for successful reproduction, the potential for accumulating multiple

mates increases with the potential for monopolizing resources. Clumped resources should therefore exhibit a high EPP.

When the temporal distribution of mates is clumped (that is, sexual receptivity in the population is highly synchronized), it becomes difficult for one individual to control numerous individuals of the other sex. This is especially true for species which exhibit a prolonged courtship. The EPP would be highest in those situations where one individual at a time is sexually receptive. A dominant male could thus utilize his energies to monopolize a sexually receptive female with little probability of losing another mating opportunity. The potential for males to accumulate multiple females should be highest in populations which exhibit asynchronous estrous periods.

The operational sex ratio provides a measure of the ease with which one sex can monopolize the limiting sex. When the proportion of sexually active males is higher than sexually receptive females, it becomes easier for a single male to gain control over this small population of females, either directly by herding or indirectly by holding and defending necessary resources. Polygyny would be favored in this case. The potential to shift towards polygyny, however, will also be affected by spatial and temporal clumping of females. When the ratio is skewed in the other direction, the tendency towards polyandry will vary with the degree of temporal and spatial clumping of males.

Evaluations of *Kerodon* and *Galea* populations by the above criteria (Table 21) indicate that both genera exhibit a high potential for polygyny. When the mating system of each genus is examined in more detail, the means by which males control females appear to differ.

Kerodon exhibits resource defense polygyny, defined by Emlen and Oring (1977) as "males control access to females indirectly, by monopolizing critical resources." The critical resource in this case is the boulder-strewn rock face, the exclusive habitat of *Kerodon*. *Kerodon* males actively defend the rock piles, and accumulate multiple mates indirectly through female choice of these limited sites.

Field and colony data strongly support this model for *Kerodon*. Field observations indicated that *Kerodon* is an extreme habitat specialist, and marked individuals maintained a fidelity to specific rock piles. *Kerodon* born in captivity had a sex ratio of unity. The sex ratio in field captured juveniles also did not differ from unity. The adult sex ratio in the

Table 21.—*Characteristics of Kerodon and Galea populations used to evaluate the ecological potential for polygyny.*

Criteria	<i>Kerodon</i>	<i>Galea</i>
Spatial distribution of resources	Highly clumped; animals occupy boulder piles which have a very patchy distribution.	Slightly clumped; more of a habitat generalist; however, always found in areas with a reasonable amount of ground cover.
Temporal distribution of mates	High to total asynchrony; females exhibit a post-partum estrous. No periodicity in the colony, no evidence of periodicity in the wild.	Moderate to high asynchrony; females exhibit a post-partum estrous. No periodicity in the colony, some evidence of periodicity in the wild.
Operational sex ratio	Highly skewed towards males; females exhibit a post-partum estrous. Males always receptive.	Highly skewed towards males; females exhibit a post-partum estrous. Males always receptive.
Precocious young	Yes.	Yes.
Limited nesting sites	Yes.	Not likely.
Paternal care	Male tolerance of juveniles in harems. No direct paternal care.	No paternal care observed.

field, however, is significantly skewed towards females (three males; 15 females, $P < 0.01$), a situation to be expected when single males monopolize a resource about which females aggregate. This result implies that the imbalance present in adults occurs only in the sexually active cohorts of the populations, in this case through intense intrasexual competition among males.

Additional behavioral observations for *Kerodon* taken in the colony are supportive. Allogrooming was observed in two contexts—adult females grooming their progeny; and juvenile males grooming the dominant male. The latter context seems to be a contact promoting gesture used by the juveniles to appease the dominant male. The male does not solicit the grooming; the juveniles cautiously approach and the dominant male remains temporarily motionless. There are no such amicable relations between the dominant male and the number two male, nor among females. It has been shown that females maintained a straight line hierarchy (Fig. 33), and relations between adult females and younger animals are predominantly agonistic. Allogrooming by the juvenile males may be of great importance in their maintaining a position in the hierarchy.

The relatively frequent use by *Kerodon* of crawl-overs, another contact-promoting behavior, may be important in maintaining social cohesiveness among harem members. Although *Kerodon* scentmarked infrequently, crawl-overs may serve to maintain an

olfactory cohesiveness among harem residents, particularly to mitigate aggressive behavior among juveniles and between adult females.

Numerous data were presented in the section on agonistic behavior which were supportive of resource defense polygyny. Hierarchy structures, rates of inter- and intrasexual aggression and use of gestures all supported the patterns expected for the maintenance of harems.

Kerodon females only became aggressive towards other females during their first pregnancy. The hierarchy that formed within the harem corresponded exactly to the order in which the female residents became pregnant. A pregnant female has much more to lose if expelled from the protection of the harem male than a non-pregnant female. Also, there was little aggression between juveniles and their mothers or the dominant male. Most aggressive interactions involving juveniles were with other juveniles and females other than their mothers. In a harem situation, a newborn would be a direct threat to these two groups. There would be direct competition with other juveniles for resources and indirect competition with other adult females in that competition with a female's progeny is a potential reduction in the fitness of that female. Nevertheless, aggression among juveniles is not as intense as might be expected. Juveniles are all related to some degree by the fact that they have a common father. If the dominant male successfully impregnates all the females, and all females have the *same number* of progeny, the average coeffi-

cient of relationship among juveniles will be equal to

$$\overline{CR} = \frac{\frac{1}{2}(p - 1) + \frac{1}{2}(N - 1)p}{Np - 1},$$

where p is the number of progeny per female and N is the total number of females in the harem. If females have unequal numbers of progeny, the average individual coefficient of relationship (I.C.R.) between any given individual and all other juveniles can be calculated as

$$\text{I.C.R.} = \frac{\frac{1}{2}(b - 1) + \sum_{i=1}^{N-1} \frac{1}{4}p_i}{\left(\sum_{i=1}^N p_i\right) - 1},$$

where b is the number of sibs of the juvenile in question. The sum of p_i in the numerator thus includes the progeny of all females except the mother of the juvenile for which the calculation is made. Both equations assume that none of the females were progeny of the dominant male. If this were to occur the relationship among juveniles would be higher. The average coefficient of relationship may be important in limiting the number of females which can form a harem. Selection would favor females and juveniles which became increasingly more aggressive towards other females and juveniles as the total number of females in the harem increased, and the average coefficient of relationship declined.

The tolerance displayed by the dominant male towards juveniles during reproductive behavior may also be linked to relatedness. By allowing his progeny to participate in the mating chase, the dominant male is essentially "grooming an heir to the throne." He allows his progeny to gain experience in developing their reproductive repertoire, and the juveniles establish a relationship with the adult female harem residents. When the dominant male dies, it is therefore more likely that one of his progeny, rather than an outside male, will assume the dominant position.

Wilson (1975) has proposed that, in harem birds, communally-breeding groups of females may be sibs, if they are genuinely cooperative. Emlen (1978) presents empirical information implying that communal females are competitive. Data collected for *Kerodon* were supportive of Emlen.

There were relatively high levels of intraharem aggression, especially among females, and between females and juveniles. Emlen (1978) predicted that, in birds, females may exploit the close proximity of

nesting areas to manipulate eggs and parasitize nests of other females. *Kerodon* females seem to manipulate progeny of other females, both by overt aggression towards juveniles as well as aggression against pregnant and lactating females. At least one juvenile death was due to a failure to lactate in the number three female. Possibly as a result of this hierarchical aggression, the dominant female produced more progeny than any of the other females. Dunbar and Dunbar (1977) reported a similar situation occurring among harem females in gelada baboons, and Downhower and Armitage (1971) have given indirect evidence that reproductive success in yellow-bellied marmots is correlated with dominance rank. Although the data presented here are hardly conclusive, it leads me to speculate that this may be a general phenomenon in harems. The question merits further, more quantitative, investigation. These observations are based upon a single colony; however, they indicate that, at least in this situation, the harem is an internally competitive group.

Galea is more difficult to classify within Emlen and Oring's system, but most closely approximates the lek type of male dominance polygyny. Males and females have overlapping territories and both sexes establish linear dominance hierarchies. Sexes do not differ either in their use of gestures or in the proportions of inter- and intrasexual aggression. Both males and females (in particular the alpha male) are aggressive towards juveniles. Dominant males apparently obtain access to estrous females by excluding other competing males through overt aggression. This is the probable reason for the significantly higher number of mean encounters in *Galea* males (Table 9).

Observations presented in the section on reproductive behavior illustrate the high level of aggression present between the dominant male and other colony males during the mating chase. The dominant male was aggressive towards all other males, including animals introduced as juveniles as well as colony-born males.

Paternal care in *Galea* is essentially nonexistent. Adult males ignore juveniles, except for occasional misdirected attempts at copulation. There is no male-male allogrooming. Other contact-promoting behaviors, especially crawl-overs, are rare. The male contribution to parental investment is also minimal. Females apparently defend their own territories and raise the young without assistance from the male. As the survival of the young is little in-

Table 22.—*Selected adaptations to an open scrub habitat in Galea spixii.*

Trait	Special function
Clawed feet	Improve traction on dusty, soft substrate
Ground forager	—
Cursorial	—
Sandbathing	Mark trails and territories on dusty substrate
Scentmarking	Mark trails and territories on dusty substrate
Large litters	Predation adaptation (see text)
Less precocious young	Trade-off for large litters
Male-subadult aggression	Maintain a dispersed distribution in the homogeneous thorn scrub habitat
Male-female linear hierarchies	Related to mating system (see text)
Large temporal allocation to foraging	Related to grass-eating habitats (see text)

fluenced by paternal care, females must choose mates either on the basis of phenotype or territory quality (Orians, 1969). Males stage aggressive contests to obtain access to estrous females, but females still make the ultimate choice, selecting the male directly, rather than indirectly, on the basis of his aggressive phenotype.

This type of polygyny requires a skewed operational sex ratio, but does not result in an unbalanced adult sex ratio. Mark-recapture data on *Galea* gave an adult sex ratio of 34 males to 26 females, which is not significantly different from unity. The sex ratio at birth is also unity.

Variance in reproductive success among males in a polygynous species is pronounced. In the specific case of harems, one male maintains multiple mates, whereas others do not mate at all. The resultant difference in reproductive success among males leads to intense intrasexual competition and perhaps to the evolution of secondary sexual characteristics (Trivers, 1972). Adult *Kerodon* males and females captured on the study area do not differ in mean weight, nor are there any obvious physical differences between males and females. The only differences observed concern the aggressive behavior described above. Sexual selection, in addition, may be mitigated in this situation by the fact that

Table 23.—*Special adaptation to boulder pile habitat in Kerodon rupestris.*

Trait	Special function
Padded feet	Improve traction on rock surface
Arboreal forager	Exploit abundant food source available in rocks (ground vegetation is minimal)
Climber	Exploit abundant food source available in rocks (ground vegetation is minimal)
Circling	Important in stopping female during mating chase (female can easily avoid male by entering rocks)
Alarm whistle	Anti-predator adaptation (see text)
Small litter size	"K-strategy" reproduction (see text)
Highly precocious young	"K-strategy" reproduction (see text)
Male subadult tolerance	Adaptation to mating system (see text)
Female linear hierarchy	Adaptation to mating system (see text)
Sally forager	Related to ability to collect a relatively large mass of food in a very short time

females choose mates indirectly, by selecting harem sites on the basis of territory quality, and not on the basis of some external secondary sexual characteristic in males. The observed differences in aggression between the sexes, however, may in some way be related to the capability of males to hold and defend rock piles.

MORPHOLOGICAL AND BEHAVIORAL ADAPTATIONS TO MICROHABITAT

I have emphasized the relationship which exists between behavioral gestures and environmental conditions. *Galea spixii* has numerous morphological and behavioral adaptations to the more open, relatively homogeneous areas it inhabits (Table 22, Fig. 39), whereas *Kerodon rupestris* is extremely well adapted for life in the boulder-strewn rock faces (Table 23, Fig. 40).

The difference in litter size and gestation period between *Kerodon* and other caviines (Table 24) indicates a possible change in reproductive strategy within the subfamily. *Kerodon* has the longest ges-



Fig. 39.—Hind foot of *Galea spixii*. Note the claws and stiff, bristly hairs; two adaptations which improve traction on sandy substrates.



Fig. 40.—Hind foot of *Kerodon rupestris*. Claws and hairs are absent, and the sole is covered with a leathery epidermal padding to improve traction on rock surfaces.

tation and smallest litter size of the caviines. *Kerodon* young are born larger and heavier than *Galea*, develop faster behaviorally (Tables 4, 5), grow faster, and, although sample sizes are small, apparently mature faster sexually (Table 6). The length of gestation period is probably related to the larger adult size of *Kerodon* in comparison with the other genera. The difference in litter size appears to be a special adaptation to the habitat.

Caviines in general occupy open formations. Births either occur in the open or in a shallow depression (Rood, 1972). There are no data indi-

cating any nest construction for Rood's Argentine caviines; however, a *Galea spixii* nest was found on the Fazenda Batente site containing an aborted fetus. The nest was constructed with dry grasses and consisted of a shallow depression with low walls. In any event, newborns and juveniles have little protection from predators.

Kerodon births occur deep in rock crevices where the danger of predation is minimal. Females nurse juveniles both in the rocks and on top of boulders; however, they are always near a crack of fis-

Table 24.—Gestation period and litter size data for various caviine species.

	<i>Kerodon</i> (this study)	<i>Galea spixii</i> (this study)	<i>Galea musteloides</i> (Rood, 1972)	<i>Cavia aperca</i> (Rood, 1972)	<i>Microcavia australis</i> (Rood, 1972)
Gestation (days)	75.0 ± 1.42	49–52	53.2 ± 0.2	60.9 ± 0.4	54.2 ± 0.4
Litter size	1.41 ± 0.5	2.2 ± 0.9	2.7 ± 0.0	2.1 ± 0.1	2.8 ± 0.3

sure when doing so. Juvenile mortality is probably much lower in *Kerodon* than in *Galea*.

All caviines give birth to precocious young. In relation to *Kerodon*, however, *Galea*, *Cavia*, and *Microcavia* have maintained relatively large litters of less precocious young. In the more open, unprotected areas inhabited by *Galea*, there is probably little advantage in having more precocious young. A juvenile, once discovered by a predator, would have little chance of escape.

Kerodon have small litters of highly precocious young which subsequently grow and develop more rapidly. Because of this rapid development and the protection offered by the habitat, juveniles mortality is lower. Females expend relatively less energy on reproduction, and would be expected to live longer and have more litters. It should be noted that litter size estimates in this study (Table 24) are probably overestimated, as nutritional levels in the colony were probably higher than in the field. No female was seen with more than one juvenile in the field.

Behavior associated with olfactory communication differed between genera. Of interest was the absence of sandbathing behavior in *Kerodon*, even though an area suitable for sandbathing was provided. Scentmarking was observed only three times. *Galea* frequently sandbathed and marked, both with urine and by dragging the perineum. These differences may be related to habitat requirements. *Galea* typically occupy open formations where the soil is granular or sandy. Runways were abundant on the study area, with numerous circular bare areas present. These areas served as foci for *Galea*'s sandbathing behavior in the wild and often contained accumulations of feces. Although suitable sandbathing areas utilized by *Galea* were at times interspersed among *Kerodon*'s rocky habitat, *Kerodon* apparently does not need to sandbathe.

The same differences of substrate may also account for the depressed frequency of scentmarking in *Kerodon*. The smooth granite surfaces would not hold a scent like the shallow, dusty depressions used by *Galea*. This would be especially true during the rainy season. However, the extensive accumulations of feces which are found in *Kerodon* populated boulder piles may have an important olfactory function. Certain piles could, in this manner, contain olfactory information about the individual residents and could provide information about territorial boundaries.

Previous attempts at relating social organization

to environmental variables have been largely unsuccessful (Clutton-Brock, 1974), primarily because comparisons have been made across widely differing taxonomic groups. Exactly how a given species adapts to a given environment will depend largely on its phylogenetic background. Such constraints have led to a variety of different responses to similar environmental problems. Basic differences in felid and canid social systems, for example, are partially related to phylogenetically old behavioral traits and morphological adaptations which influence hunting strategies (Kleiman and Eisenberg, 1973).

In order to evaluate the importance of environmental factors on social organization it is far more profitable to examine closely related species which occupy markedly different habitats. Barash (1974) was successful in correlating differences in social organization with environmental factors for three species of *Marmota*.

Hoeck (1975) studied two sympatric species of rock hyraxes, *Procavia johnstoni* and *Heterohyrax brucci*, in Tanzania. Both species have similar morphology and social structure, although *Procavia* is somewhat larger. Both species are highly modified for life in the kopjes (rock outcroppings) of the African plains, and the males of both species maintain harems. The hyraxes represent a situation where the extensive morphological adaptations they have undergone limit them to a certain habitat type, much like *Kerodon*. Existence in the rock piles, a clumped resource, has favored the evolution of a harem-based mating system in both genera. In the case of the hyraxes, the only behavioral modification to allow for coexistence has been the development of differential feeding behavior in the two genera. *Heterohyrax* browses predominantly on trees and shrubs, whereas *Procavia* is predominantly a grazer. The hyraxes illustrate an example where both morphology and habitat place restrictions on the degree in which social behavior is modified. Although both genera are physically capable of feeding in shrubs (*Procavia* in fact does browse during the dry season), the modified foraging behavior in *Procavia* may be important in facilitating coexistence between the two genera.

The strong morphological and behavioral similarities between *Kerodon* and the hyraxes demonstrate an interesting example in convergence. Both the hyraxes and *Kerodon* are tail-less, guinea pig-like animals with padded feet. Both have four clawless toes on the forepaws and three on the hindfeet,

the innermost toe being equipped with a small grooming claw. The hyraxes, subungulates, have rodent-like skulls with elongated rostrae, very much like the skull of *Kerodon*. Both groups occupy rock piles, and both have harem-based mating systems. Both even demonstrate the peculiar trait of defecating only in certain areas of the rock piles.

A number of other rock-dwelling mammals of widely differing phylogenetic backgrounds have also evolved the same specialized morphology—pikas (Ochotonidae), gundis (Ctenodactylidae), and yellow-bellied marmots (Sciuridae). The marmots (*Marmota flaviventris*) have also been studied behaviorally and possess a harem-based mating system (Armitage and Downhower, 1974; Armitage, 1975). Detailed behavioral studies on pikas and gundis would provide valuable information on the importance of social behavior in ecological adaptation.

I have argued that two closely related species show quite distinct patterns of social organization in response to differing environmental pressures. The paleontological work of Pascual (1962) indicat-

ed that the genera *Galea* and *Kerodon* were more closely related to each other than either was to *Cavia* or *Microcavia*. If behavioral differences closely reflected taxonomic affinities, *Kerodon* and *Galea* would have exhibited more similar behavioral repertoires and social organizations than *Galea* and either *Cavia* or *Microcavia*. The fact that *Galea* exhibited more similarity to the other open formation caviines (*Cavia* and *Microcavia*) implies that behavioral repertoires are responsive to ecological conditions. The rather strict habitat requirements of *Kerodon* were reflected in associated behavioral traits.

Social organization thus appears to be strongly associated with ecological adaptation. This implies a far greater flexibility in the genetic control of behavior (or a far greater genetic variability) than, for example, with morphology. Whereas morphology provides the "basic hardware" of ecological adaptation, the lability of the behavioral response allows an organism to fine tune its interrelationship with the environment.

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APPENDIX I

Botanical survey of the Fazenda Batente study site. Plant identifications done by Drs. Dardano de Andrade Lima and Marcelo de Ataíde Silva of the Instituto de Pesquisas Agronômicas in Recife, Pernambuco, Brazil.

Family	Scientific name	Common name
Acanthaceae	<i>Jacobina</i> sp.	Canela de nambu
	<i>Ruellia asperula</i>	Câmara branco
	<i>Ruellia paniculata</i>	Câmara
	<i>Ruellia bahiensis</i>	
	<i>Ruellia</i> sp.	Câmara de boi
Amaranthaceae	<i>Amaranthus spinosus</i>	Bredo de porco
Anacardiaceae	<i>Astronium urundeuva</i>	Aroeira
Boraginaceae	<i>Cordia globosa</i>	Maria prêta
	<i>Cordia insignis</i>	Orelha de Leão
Bromeliaceae	<i>Encholyrium spectabile</i>	Croata
Byttneriaceae	<i>Waltheria</i> sp.	Malvinha
Cactaceae	<i>Cereus jamacaru</i>	Mandacaru
	<i>Pilosocereus gounellei</i>	Xique-xique
	<i>Pilosocereus piauhyensis</i>	Facheiro
	<i>Arrojadoa rodantha</i>	Rabo de raposa
	<i>Opuntia palmadora</i>	Palma
Capparaceae	<i>Crataeva tapia</i>	Trapia
Commelinaceae	<i>Commelina</i> sp.	Cipó
Compositae	<i>Centratherum punctatum</i>	Peripeta
	<i>Blainvillea rhomboidea</i>	Bamburra
Convolvulaceae	<i>Ipomoea sobrevoluta</i>	
	<i>Ipomoea</i> sp.	Gitirana
Cucurbitaceae	<i>Cayaponia tayuya</i>	Tajuja
	<i>Mamordica charantia</i>	Melão de São Caetano
	<i>Cucumis anguria</i>	Maxixe
Cyperaceae	<i>Cyperus</i> sp.	Capim barba de bode
Erythroxylaceae	<i>Erythroxylum</i> sp.	Pau vidro
Euphorbiaceae	<i>Croton jacobinensis</i>	Marmeleiro
	<i>Croton campestris</i>	Velame
	<i>Croton argyrphyloides</i>	Casatinga
	<i>Cnidoscolus urens</i>	Cansacão
Flacoutiaceae	<i>Prockia crucis</i>	
Gramineae	<i>Rhynchelytrum repens</i>	Capim rosado
	<i>Panicum</i> sp.	Capim touceira
	<i>Aristida</i> sp.	Capim mimoso
	<i>Cenchrus echinatus</i>	Capim carrapicho
	<i>Brachiaria mutica</i>	Capim de planta
Guttiferae	<i>Vismia guianensis</i>	Lacre
Labiatae	<i>Leonotis nepetaefolia</i>	Cordão de São Francisco
	<i>Hyptis pectinata</i>	Bamburra
	<i>Hyptis</i> sp.	Câmara branco
Leguminosae	<i>Piptadenia zehntneri</i>	Angico brabo
	<i>Piptadenia</i> sp.	Espinheiro Prêto
	<i>Cassia excelsa</i>	Canafistula
	<i>Pterogyne nitens</i>	Madeira Nova
	<i>Erythrina velutina</i>	Mulungu
	<i>Indigofera suffruticosa</i>	Anil de bode
	<i>Microptilium longepedunculatum</i>	Orelha do Preá

APPENDIX I—Continued

Family	Scientific name	Common name
	<i>Phaseolus semierectus</i>	Orelha do Preá
	<i>Phaseolus peduncularis</i>	Feijão de rolinha
Malvaceae	<i>Gaya</i> sp.	Melosa
	<i>Bogenhardia tiubae</i>	Melosa
	<i>Sida paniculata</i>	Malva prêta
	<i>Sida galheirensis</i>	Malvinha
Meliaceae	<i>Cedrela</i> sp.	Cedro
Portulacaceae	<i>Portulaca elatior</i>	Bedoegua de ovelha
Rhamnaceae	<i>Rhamnidium</i> sp.	
	<i>Ziziphus joazeiro</i>	Juá
Rubiaceae	<i>Mitracarpus</i> sp.	Peripeta
Sapindaceae	<i>Sapindus saponaria</i>	Sabonete
	<i>Talisia esculenta</i>	Pitombeira
	<i>Cardiospermum halicacabum</i>	Chocalho de vaqueiro
	<i>Serjania caracasana</i>	Cipó saltocora
	<i>Serjania</i> sp.	Cipó folha de carne
Scrophulariaceae	<i>Scoparia dulcis</i>	Vassourinha
Solanaceae	<i>Solanum paniculatum</i>	Jurubeba
	<i>Solanum americanum</i>	Erva moura
	<i>Lycopersicon esculentum</i>	Tomate brabo
Vitaceae	<i>Cissus simsiana</i>	Parreira
	<i>Cissus sicyoides</i>	Cipó mole

APPENDIX II

PROTOCOLS OF REPRODUCTIVE BEHAVIOR FOR *KERODON* AND *GALEA**Galea Protocol*

24 March 1978–10:05 PM: The dominant male (MR) began following female B3, attempting to place his chin on the female's rump. B3 gave a tail-up, spraying urine on MR. MR shook his head back and forth, and continued following B3. The number two male, BM, twice tried to join the chase, once taking the lead, but both times was aggressively chased by MR.

MR then directed aggressive lunges toward three males: BM, BF, and FMR. MR resumed the chase, following B3 through the rock piles, always attempting to place his chin on her rump. MR would occasionally attempt to bite the rump of B3, in an apparent attempt to halt her flight. During the chase B3 passed female M, and as MR approached M, she gave a tail-up and in quick succession twice urinated on MR. MR retreated and groomed.

MR resumed the chin-rump follow on B3, and as he passed close to M, she gave a tail-up and MR avoided her. MR then walked towards the middle of the room using short, deliberate strides, pausing as he strode, then lunged at FMR. A contagious chorus of peepy squeaks had overtaken the colony. MR lunged again at FMR, then sat down in the sandbathing arena. MR rose and lunged at BF, then at BM; then began chin-rump following B3 again. As before, at every opportunity MR attempted to chin the rump of B3. Other males were obviously excited, but MR re-

stricted them from entering the chase. MR again attempted to bite the rump of B3.

Male BF, excited by the mating chase, began to follow female B13. MR immediately stopped following B3 and lunged at and bit BF. MR then lunged at B13. MR directed a series of especially violent lunges at BF. BF then lunged at juvenile male B2M.

MR began a chin-rump follow, this time on B13, attempting to mount after placing his chin on her rump. Each time MR placed his chin on the rump of B13, she paused, and MR attempted to mount. B13 then moved away, and MR reinitiated the follow.

The other colony males were obviously excited, but could not approach B13. MR lunged at BM, then at BF. MR relinquished the chase, went up on the rock pile, and began to bark. The activity level rapidly declined. MR groomed himself, and continued barking. B13 began to answer the low bark of MR with a higher-pitched, peepy bark. Male FMR attempted to approach B13, and was attacked by MR.

Kerodon Protocols

A) 28 September 1977–10:35 AM: Female F came out of the rear rocks, and the dominant male FR ran back to her and sniffed

the vaginal area. They separated. At 10:46, FR entered the rocks where F was sitting; a few seconds later she emerged and FR followed with his chin on her rump. She re-entered the rear rocks, and FR sat on top, face-wiped twice, and then returned to the central rock pile.

At 10:55, the number two male, R, descended from his perch in a tree and entered female F's rocks. After a delay of a few seconds, she emerged and circled back into the rocks, with R following. As they entered the rocks, R attempted to mount F. FR almost immediately ran back and chased R from the presence of F.

- B) 28 September 1977-3:40 PM: Male R approached female F and sniffed the vagina. He then attempted to mount and she resisted. FR immediately arrived and chased R. R climbed one of the trees in the colony room, and FR climbed another. FR descended, ran over to the tree in which R was perched, and chased R from the tree. R then ran over to female F and attempted to mount a number of times. The dominant male then aggressively chased female F from the area. FR then began to follow F, always attempting to mount. He then mounted successfully, with intromission, thrusting five or six times. The number two male, R, then approached and lunged at FR, who was still mounting female F. FR turned on R, who fled.

FR then sat behind F, who exposed her perineum to FR, apparently receptive. FR then began to follow F, attempting to mount, but the female continually moved away.

R again approached the female, and gave a series of twisting lunges, attempting to separate the male from the female. FR, however, would not leave F.

At 3:50 PM, the activity level declined. R climbed a colony tree, and after a short delay, FR climbed the same tree and began a series of three prolonged aggressive chases on R. After the last chase, R fled at the mere approach of FR.

- C) 3 October 1977-3:58 PM: Dominant male FR sat at female B's left side and placed his chin on her back. FR then circled, again placed his chin on the female's back, circled again and gave a naso-anal. Female B began to move away and FR followed. Subadult male J2 immediately joined in, and male BR also began to follow after about 30 seconds. The follow deteriorated into an all out chase, with B fleeing and all three males pursuing in an odd hopping, "stotting" gait. FR was generally in front, although J2 at times took the lead. Whenever the leader was sufficiently close to B, he would place his chin on the rump. The leading male would often try to

hop on the fleeing female and mount. The chase then diminished in intensity and ended at 4:00 PM. At 4:02 FR approached female B, gave a naso-anal, and attempted to mount. B then moved away from FR and J2 attempted to mount. B lunged at J2, who fled. Subadult male BR then approached the dominant male and gave a naso-anal and attempted to mount. FR merely moved away.

At 4:07, an all out follow-chase began again, initiated by FR sniffing the back and rump of B. Was chased by FR, J2, and BR; with the latter attempting to mount FR. B had little trouble in avoiding all three males. The follow-chase stopped briefly, then began again at 4:18; same participants and same behavior. BR again attempted to mount FR.

FR continued to chase B, who ran a bit, then stopped and presented a tail-up with urine-squirting. FR stopped, shook his head to and fro, and face-wiped. After a delay of about 10 minutes, FR and J2 resumed the chase on B. B again responded with a series of tail-ups. J2, however, managed to mount, and achieved intromission, but there was no thrusting.

Short chase on B by all three males again took place at 4:36, 4:43, and 4:45. During the third chase, FR seemed confused and began to follow a non-estrous female, F. As soon as he got sufficiently close, however, he turned away. At one point while being followed, B turned and lunged at BR. FR and BR continued the pursuit. The female actually had no difficulty in avoiding the pursuing males. B climbed a tree and the males temporarily desisted. At 4:50 B descended, and FR again initiated the chase. BR attempted to mount FR, who turned on BR in an upright aggressive posture. J2 then began to follow B, and BR attempted to mount him also. At 4:53 this last chase deteriorated, and the activity level quickly decreased.

- D) 2 December 1977-7:30 AM: J2 repeatedly attempted to mount subadult female JR. At J2's approach, JR would assume a submit posture; J2 then giving a naso-anal. J2 would place his chin on the rump of JR and attempt to mount. JR would pull away, J2 riding the female for a short distance. After a series of attempted mounts by J2, BR approached and chased J2, then began to follow JR. The two males then followed alternately, with a high frequency of circling. The male would approach the female and give either a naso-anal or a nose-nose, then would begin circling. While being followed, JR would avoid the males, but she remained motionless while being circled; either standing, sitting or in the submit posture.